SKELETAL VARIATION IN MELANESIAN FOREST FROGS (ANURA: CERATOBATRACHIDAE)

BY

ALLISON M. FUITEN

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Chairperson Dr. Linda Trueb

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Dr. Rafe Brown

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Dr. Paulyn Cartwright

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The Thesis Committee for Allison M. Fuiten

certifies that this is the approved version of the following thesis:

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ABSTRACT:

Ceratobatrachidae is a ranoid family, which includes at least 87 described anuran species in six genera. Recent large-scale molecular phylogenies of Ranidae have shown strong support for the family's monophyly and 85 of the 87 described species can be divided into two primary monophyletic evolutionary radiations—one involving 30 Philippine species and another including 55 species from the islands of New Guinea, Palau, Fiji, and the Solomon-Bismarck Archipelago. I described osteological variation in eleven species of ceratobatrachids that occupy different microhabitats in both radiations in order to survey the amount of osteological diversity and identify convergent skeletal modifications repeated within this family. Although it is clear that certain morphological traits are a reflection of the shared phylogenetic history of the group, other characters are found to correspond to the ecology of the frog and therefore are the result of proximate adaptation to the immediate environment.

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INTRODUCTION

DESPITE the relatively uniform overall body plan, different anuran groups show considerable variation in their skeletal structures. The skeletal modifications identified at the specific levels can significantly contribute to systematic and phylogenetic inference within anurans, but must be used carefully because they are highly susceptible to convergent development and adaptation to the surrounding environment (Trueb, 1973).

Ranoids of the family Ceratobatrachidae are an ideal group with which to explore questions of morphological specialization and skeletal convergence at the specific levels. Thought to have originated on the Antarctic-Australia-New Guinea landmass, the current distribution of Ceratobatrachidae is confined to New Guinea, Fiji, Bismarck Archipelago, Palau, Solomon Islands, Philippines, and Borneo (Allison, 1996; Brown, 1997; Bossuyt et al., 2006). This diverse family includes 30 Philippine species in the genus *Platymantis*, two species of *Ingerana* found in the Philippines and Borneo, and another 55 Papuan/Solomon-Bismarck species in five genera: eight species of *Batrachylodes,* one species of *Ceratobatrachus*, five species of *Discodeles,* one species of *Palmatorappia*, and an additional 40 species of *Platymantis* (Brown et al., 1997b; Kraus, 2008; Frost, 2011; AmphibiaWeb, 2012) (Fig. 1; see Appendix 1). All species of Ceratobatrachidae lay eggs outside of water and undergo direct development.

Recent molecular phylogenies of Ranoidea show that the genera *Platymantis*, *Batrachylodes*, *Discodeles*, *Palmatorappia*, and *Ceratobatrachus* represent a monophyletic group that is sister to the two Southeast Asian species of *Ingerana*. The species of the genera *Platymantis*, *Batrachylodes*, *Discodeles*, *Palmatorappia*, and *Ceratobatrachus* belong either one of two separate radiations—a Philippine radiation and a Papuan/Solomon-Bismarck radiation — with arboreal, terrestrial, and semi-aquatic ecomorphs having evolved independently in each

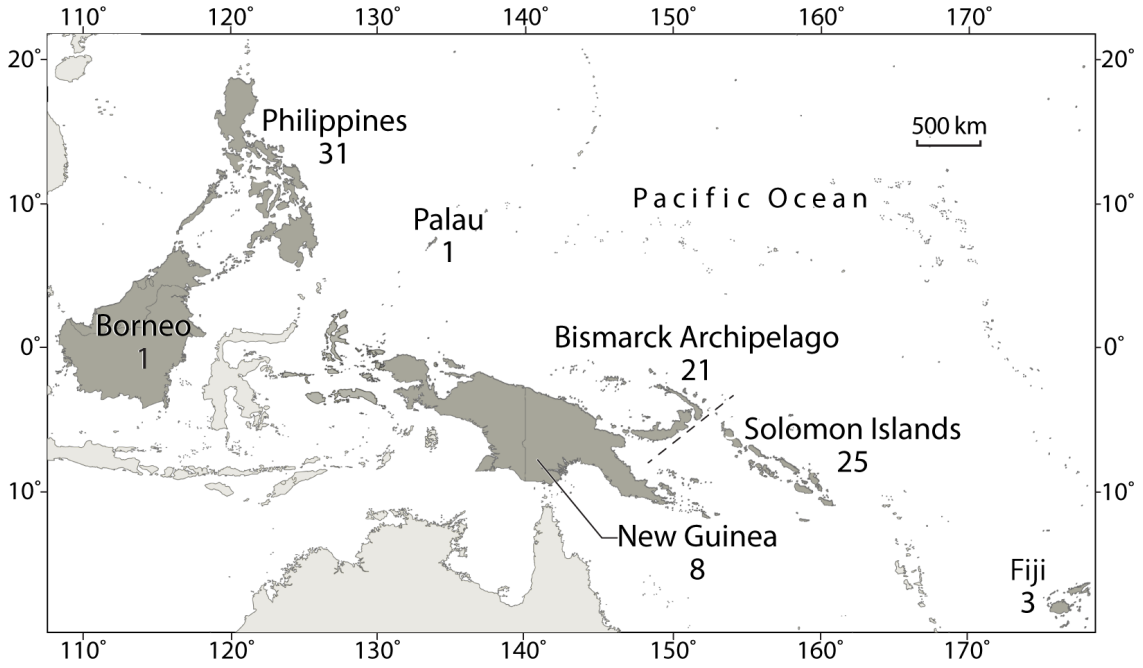

FIG. 1.—Map illustrating the distribution of species of Ceratobatrachidae in Southeast Asia. The number of described species found in each region is listed under the country or geographic region name. The dashed line indicates the borders between the Bismarck Archipelago from the Solomon Islands. *Discodeles guppyi* and *Platymantis solomonis* are currently found in both the Solomon Islands and the Bismarck Archipelago and *Platymantis papuensis* is found in both the Bismarck Archipelago and New Guinea.

radiation multiple times (Brown, 2004). Together, these 87 species, plus numerous undescribed taxa (Brown et al., 2008), constitute the family Ceratobatrachidae (Brown, 2004; Bossuyt et al., 2006; Wiens et al., 2009; Pyron and Wiens, 2011).

In this study, I provide detailed osteological descriptions of eleven species of ceratobatrachids frogs, with the goal of identifying convergent skeletal features and describing the extent of skeletal diversity within the family. The surveyed species represent the range of morphological and ecological variation present in both radiations.

Taxonomic History

Günther first described *Platymantis* in 1859, removing it from Duméril's *Hylodes* (1853). *Platymanis* originally was distinguished from the sympatric genus of *Cornufer* Tschudi (1838) based on degree of terminal disk expansion. Inger synonymized *Platymantis* with *Cornufer* in 1954 and asserted that degree of digital expansion was insufficient to distinguish the two genera. Later, the name *Cornufer* was suppressed and *Platymantis* was used instead when it was discovered that the holotype for *Cornufer* was in fact a specimen from the New World genus *Eleuthodactylus* (Zweifel, 1967).

Boulenger, in his series of taxonomic papers describing the herpetofauna of the Solomon Islands, described the monotypic genus *Ceratobatrachus* and another genus, *Batrachylodes* (1884, 1887). In addition, he reported *Discodeles* as a subgenus of *Rana* (1884). Boulenger (1918) distinguished *Discodeles* from other subgenera of Southeast Asian *Rana* based a suite of characters, which included presence of large nasal bones and a forked omosternum; Noble elevated *Discodeles* to the level of genus (Noble, 1931). Barbour (1921) considered Ceratobatrachinae as a subfamily of Ranidae asserting that a single character (teeth present in the upper and lower jaw) was insufficient to justify retaining Ceratobatrachidae as a separate family. Finally, Ahl (1927) redescribed *Hylella solomonis* (Sternfeld, 1918) as *Palmatorappia solomonis*, moving it from Hylidae to Ranidae because of the presence of a forked omosternum.

Inger (1954) moved *Ingerana baulensis* from the *Cornufer* to *Micrixalus* because of its extensive webbing, absence of tubercles on the metacarpals and round shape digital disks. At the same time, Inger described a new species—*Micrixalus mariae*—and noted that it must be closely related to *M. baulensis* because of their extremely similar morphology. *Ingerana* was erected by Dubois (1986), who transferred *Micrixalus mariae* and *M. baluensis* into *Ingerana*, along with

several other ranid species, based on a suite of morphological characters that included small body size, forked omosternum, and T-shaped terminal phalanges. Species of *Ingerana* are currently placed in two ranoid families and require taxonomic revision. *Ingerana baluensis* of Borneo and *Ingerana mariae* of the Philippines are considered part of Ceratobatrachidae, while the other members of *Ingerana* (all found on mainland Asia) are distantly related and currently placed in Dicroglossidae (Bossuyt et al., 2006; Wiens et al., 2009; Pyron and Wiens, 2011).

Authors of previous morphological studies hypothesized that these genera were closely related. Boulenger noted in a footnote that *Cornufer* was derived from *Discodeles* (1918). Noble (1931) discussed morphological similarities among the genera and suggested that *Ceratobatrachus guentheri* must be closely related to the species of *Platymantis* because of their relatively large crania, small digital disks, reduced interdigital webbing, and similar pectoral girdles. He also described *Discodeles* as most morphologically similar to *Platymantis*, with only the larger amount of webbing and presence of obtuse papillae on the center of the tongue on *Discodeles* distinguishing the two genera from each other. Additionally, Noble (1931) noted that both *Palmatorappia solomonis* and species of *Batrachylodes* lack vomerine teeth. When Boulenger (1896) originally described *Ingerana baulensis*, he placed it in the genus of *Cornufer*. Before Dubois' taxonomic revision in 1986, Inger (1954) placed *Ingerana mariae* and *I. baulensis* in Noble's subfamily, Cornuferinae, which at that time also included *Platymantis*, *Discodeles*, *Cornufer*, *Ceratobatrachus*, and *Batrachylodes*. The presence of a forked omosternum, large nasals, firmisternal girdles, and direct development has repeatedly been used as unifying characters for the genera of Ceratobatrachidae (Noble, 1931; Deckert, 1938; Brown, 1949, 1952; Dubois, 1975, 1986).

The first osteological description of a ceratobatrachid species—*Ceratobatrachus guentheri*—highlighted a relatively standard ranoid skeleton with a bifurcated omosternum (Boulenger, 1886). Subsequent, limited osteological observations have been consisted mainly of notes on the omosternum, sternum, relative size of nasals, and presence or absence of vomerine teeth (Roux, 1905; Barbour, 1921; Noble, 1931; Deckert, 1938; Brown, 1952; Dubois, 1975, 1986). Norris (2002), as part of a phylogenetic analysis that included analysis of osteological characters, provided descriptions of the osteology of frogs of the Solomon Islands, including species from *Palmatorappia*, *Batrachylodes*, *Platymantis*, *Discodeles*, and *Ceratobatrachus*.

MATERIALS AND METHODS

Ten cleared-and-stained specimens of *Platymantis* were examined along with six additional specimens representing non-*Platymantis* taxa (see the Appendix 2). Selection of representative taxa focused on sampling the extremes of morphological and ecological variation observed in the family (Brown, 2004; RMB, pers. obs.).

I chose the following taxa for osteological descriptions. *Platymantis dorsalis* is a terrestrial ecomorph from the Philippine radiation and *Pl. solomonis* is a terrestrial ecomorph from the Papuan radiation. *Platymantis guentheri* and *Pl. guppyi* are arboreal tree canopy ecomorphs from the Philippine and the Papuan/Solomon-Bismarck radiations, respectively. *Platymantis hazelae*, a Philippine arboreal shrub ecomorph, also was included along with *Ceratobatrachus guentheri* (a large-bodied, terrestrial, highly camouflaged "leaf mimic" species) and *Batrachylodes trossulus* (a small-bodied terrestrial species from the Papuan radiation). *Palmatorappia solomonis* was chosen as a small-bodied tree frog (analogous to the arboreal shrub frogs of the Philippines). *Batrachylodes vertebralis* is a small scansorial shrub specialist, chosen because of its preferred arboreal microhabitat. I selected *Discodeles bufoniformis* (a large Solomon-

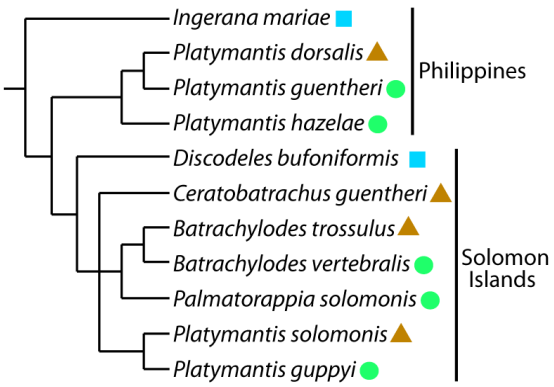

FIG. 2. —Clagogram depicting the phylogenetic relationships of taxa used in this study based on Pyron and Wiens (2011) and Brown (2004). Brown triangles indicate the species that are terrestrial ecomorphs, green circles indicate species that are arboreal ecomporhs, and blue squares indicate species that are semi-aquatic ecomorphs.

Bismarcks species) and *Ingerana mariae* (a medium-sized Philippines species, closely related to *I. baluensis* from Borneo; Bossyut et al., 1996) because both prefer semi-aquatic habitats (Fig. 2).

Snout–vent lengths (SVL) were measured to the nearest 0.1 mm with digital calipers before the frogs were cleared-and-stained. Snout–vent lengths of previously cleared-and-stained specimens *B. vertebralis*, *C. guentheri* and *Pa. solomonis* are not available. Techniques for clearing and double-staining follow those of Klymkowsky and Hanken (1992), which differentially stain cartilage blue (Alcian blue) and bone red (Alizarin red), while making the soft tissues translucent. Observations and illustrations were made with a stereo dissection microscope equipped with a camera lucida. Proportional descriptions (defined in Figs. 3 and 4) are based on measurements of individual skeletal elements, taken with digital calipers. The average of three independent measurements was used for all calculations of proportions.

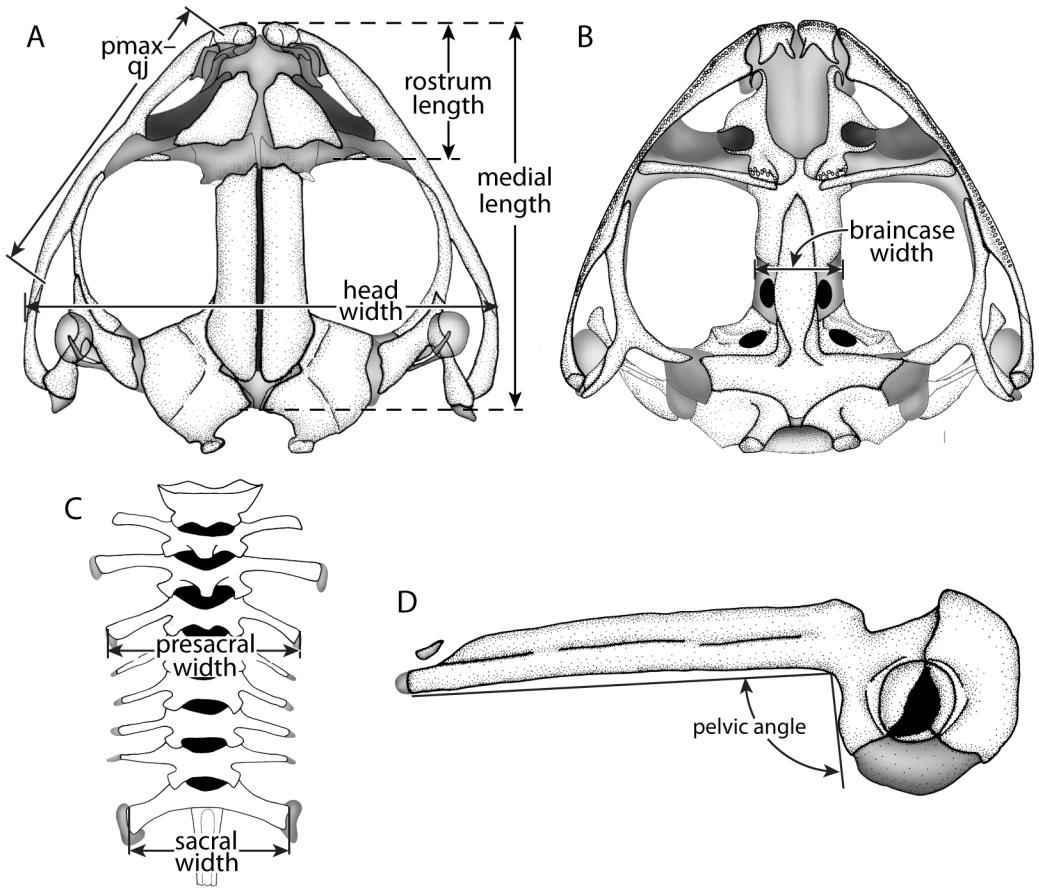

FIG. 2.—Cranial measurements in dorsal (A) and ventral (B) aspects, vertebral column widths (C), and pelvic angle (D) examined.

Osteological descriptions are based on male specimens, with the exceptions of *Batrachylodes trossulus* and *Pa. solomonis* for which only female cleared-and-stained specimens were available. Terminology of osteological elements follows that of Trueb (1973), Duellman and Trueb (1994) and Fabrezi and Alberch (1996).

RESULTS

Osteological Descriptions

The following osteological descriptions are based on a cleared-and-double stained adult males of *Platymantis dorsalis* (KU 313709, SLV = 28.48 mm), *Pl. hazelae* (KU 306739, SLV = 21.48 mm), *Pl. guentheri* (KU 319619, SLV = 28.05 mm), *Pl. solomonis* (KU 307121, SLV =

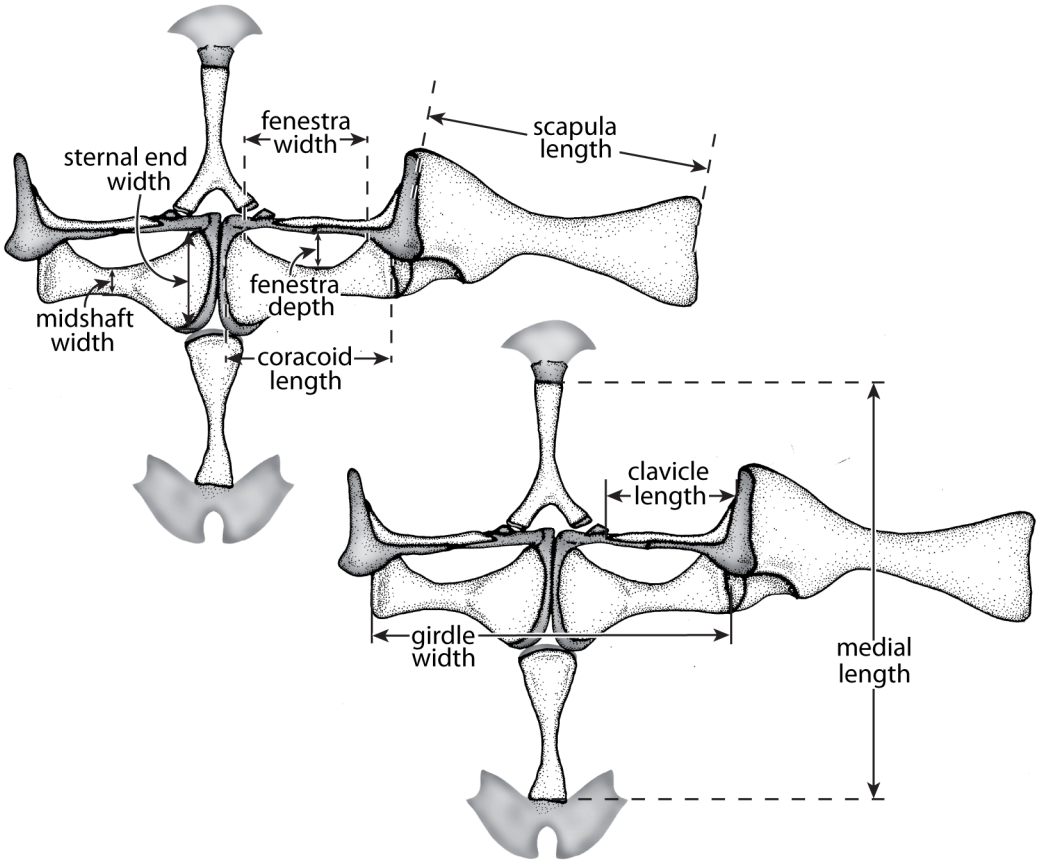

FIG. 3.—Pectoral girdle measurements and proportions examined.

43.19 mm), *Pl. guppyi* (KU 98161, SLV = 48.64 mm), *Batrachylodes trossulus* (KU 145134, SVL = 20.38 mm), *B. vertebralis* (KU 93735, SVL unknown), *Palmatorappia solomonis* (KU 93749, SVL unknown), *Ceratobatrachus guentheri* (KU 98467, SVL unknown), *Discodeles bufoniformis* (KU 307262, SVL = 73.61 mm), and *Ingerana mariae* (KU 309472, SLV = 27.89 mm).

Cranial Osteology

Cranial shape and proportions (Figs. 5–15; Table 1).—The skull is widest at the level of the articulation of the maxilla with the quadratojugal in all taxa examined, and wider than long. *Ingerana mariae*, *C. guentheri*, *D. bufoniformis*, and *Pa. solomonis* have wider skulls (HL <

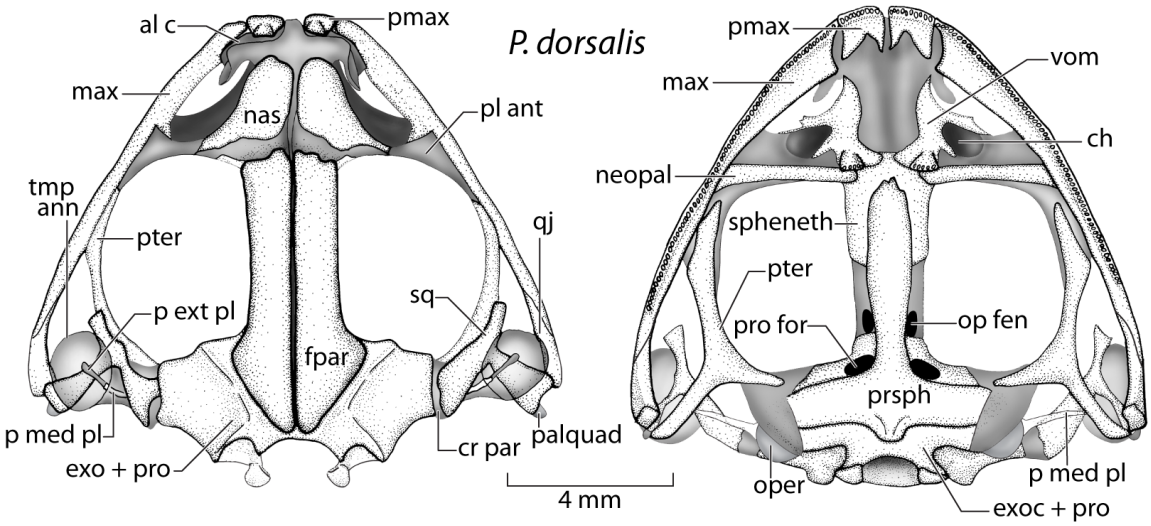

FIG. 4.—Crania: *Platymantis dorsalis* (KU 313709) in dorsal (left) and ventral (right) aspects. Black and white stipple represents bone, gray tone is cartilage, and stippling in gray represents mineralization of the cartilage. al c, alary cartilage; ch, choana; cr par, crista parotica; exo + pro, fused exoccipital and prootic; fpar, frontoparietal; max, maxilla; nas, nasal; neopal, neopalatine; op fen, optic fenestra; oper, operculum; p ext pl, pars externa plectri; p med pl, pars media plectri; palquad, palatoquadrate; pl ant, planum antorbitale; pmax, premaxilla; pro for, prootic foramen; prsph, parasphenoid; pter, pterygoid; qj, quadratojugal; spheneth, sphenethmoid; sq, squamosal; tym ann, tympanic annulus; vom, vomer.

85%) than *P. hazelae*, *P. dorsalis*, *P. guentheri*, *Pl. solomonis*, *P. guppyi*, *B. trossulus*, and *B. vertebralis* (HL > 85%). Greatest height on skull in lateral view is at the posterior edge of the frontoparietal in all species. *Discodeles bufoniformis* and *P. guppyi* have relatively flatter skulls (greatest height 29–32% of length of anterior tip of premaxilla to posterior tip of quadratojugal) than *I. mariae*, *C. guentheri*, *Pa. solomonis*, *B. vertebralis*, *B. trossulus*, *P. dorsalis*, *P. guentheri*, *P. hazelae* and *Pl. solomonis* (greatest height 37–43% of length of premaxilla to posterior tip of quadratojugal).

The rostra are slightly shorter in *B. trossulus* and *B. vertebralis* (30% and 32% HL, respectively; 31% and 32% of anterior tip of premaxilla to posterior tip of quadratojugal, respectively) than in the other nine species (35–44% HL; 38–33% of anterior tip of premaxilla

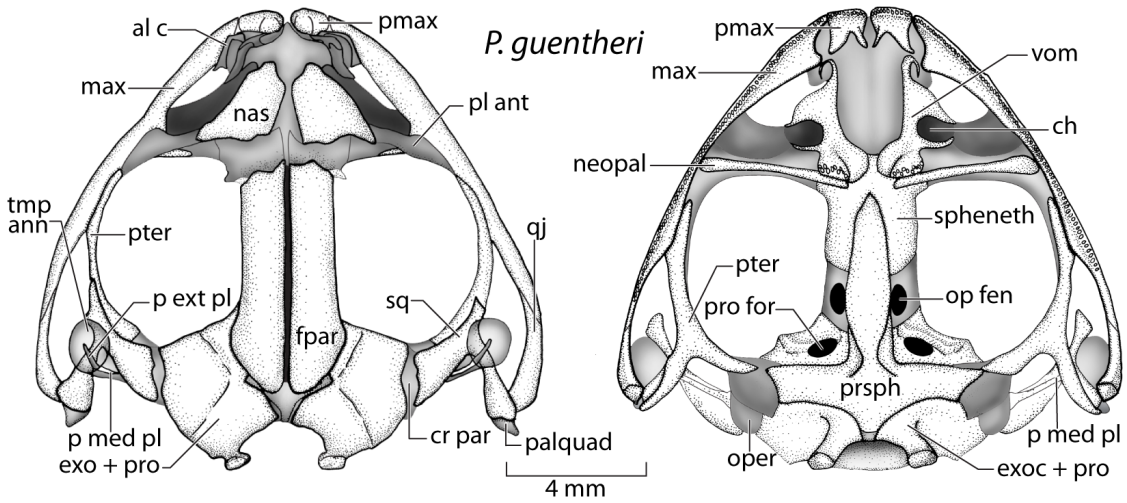

FIG. 5.—Crania: *Platymantis guentheri* (KU 319619) in dorsal (left) and ventral (right) aspects. Black and white stipple represents bone, gray tone is cartilage, and stippling in gray represents mineralization of the cartilage. Abbreviations as in Figure 5.

to posterior tip of quadratojugal).

Discodeles bufoniformis and *Platymantis solomonis* have narrower braincases (width of the braincase from ventral view at the level of the mid-orbit 19% and 22% HL, respectively) than do the remaining taxa (25–34% HL). The mid-orbital width of the braincases varies from 20–29% of the greatest width of the skull in all taxa except *D. bufoniformis*, in which the braincase is only 16% of the greatest width of the skull.

Neurocranium (Figs. 5–15; Table 1).—The anterior neurocranium, composed of the large olfactory capsules and anterior part of the braincase, is predominantly cartilaginous in all species. The septum nasi is wider and longer in *P. hazelae* and *Pa. solomonis* than in *P. guentheri*, *P. dorsalis*, *P. guppyi*, *Pl. solomonis*, *D. bufoniformis*, *I. mariae*, *B. trossulus*, and *B. vertebralis* and is not visible dorsally in *C. guentheri*. The single internasal septum terminates anteriorly in a distinct median prenasal process in all species. The plana antorbitalae are robust, cartilaginous structures with a transverse orientation in all taxa except *C. guentheri*. Each is invested by the neopalatine ventrally. In *C. guentheri*, the plana antorbitale is ossified to the

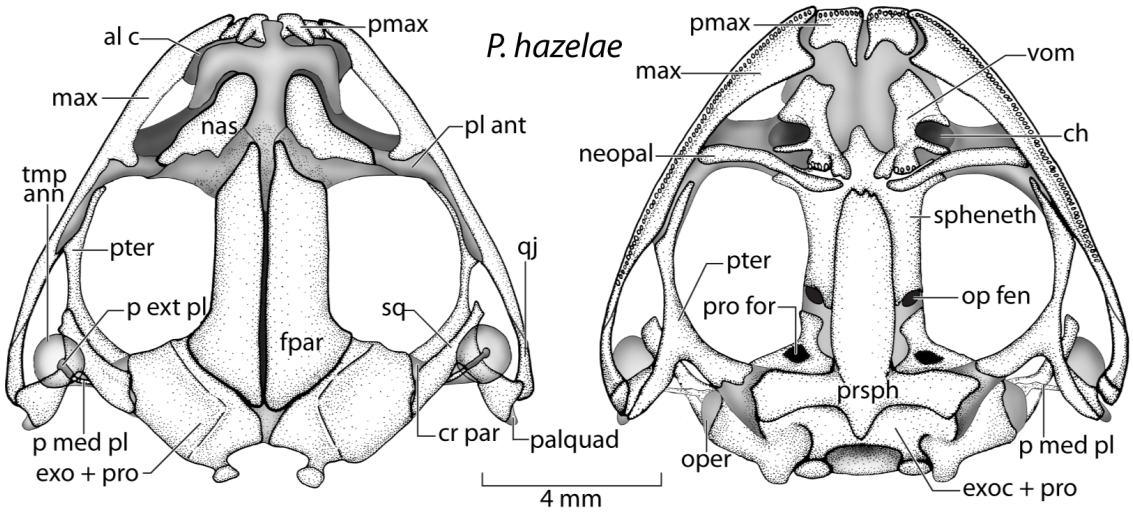

FIG. 6.—Crania: *Platymantis hazelae* (KU 306739) in dorsal (left) and ventral (right) aspects. Black and white stipple represents bone, gray tone is cartilage, and stippling in gray represents mineralization of the cartilage. Abbreviations as in Figure 5.

maxilla without visible sutures.

The medial margins of the nasal capsules are widely separated for *P. hazelae* and *Pa. solomonis* in contrast to *P. dorsalis*, *P. guppyi*, *Pl. solomonis*, *D. bufoniformis*, *I. mariae*, *B. trossulus*, and *B. vertebralis* which have narrowly separated medial margins of the nasals. *Platymantis guentheri* is the only taxon that the medial margins of the nasal diverge from each other, resulting in the posterior end being widely separated and the anterior end narrowly separated. The medial margins of the nasal capsules abut in *C. guentheri*. The bones are triangular with blunt anterior margins in all species. In only *Pl. solomonis* and *P. guentheri* the nasals are notched on the anterodistal margins, whereas the posterior margins are only irregularly scalloped in *Pl. solomonis* and *P. guppyi*. The nasals are moderately separated from the frontoparietals in *P. guentheri*, *P. dorsalis*, *P. hazelae*, and *P. guppyi* compared to *Pl. solomonis*, *B. vertebralis*, *B. trossulus*, *I. mariae*, *D. bufoniformis*, and *C. guentheri* (narrowly separated). Only in *Pa. solomonis* are the nasals broadly separated from the frontoparietals.

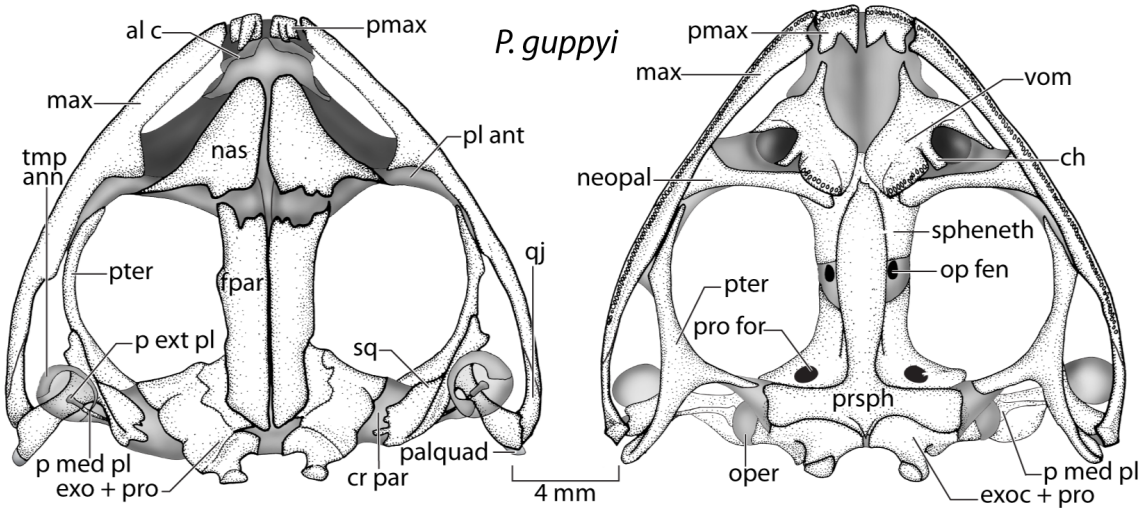

FIG. 7.—Crania: *Platymantis guppyi* (KU 98161) in dorsal (left) and ventral (right) aspects. Black and white stipple represents bone, gray tone is cartilage, and stippling in gray represents mineralization of the cartilage. Abbreviations as in Figure 5.

Alary cartilage is visible in dorsal view in all eleven species and lie posteroventrally from the medial prenasal processes. A medial prenasal process is present in all eleven species.

The parasphenoid is shorter in *Pa. solomonis*, *C. guentheri*, *B. trossulus*, and *B. vertebralis* than in the other seven taxa. The end of the cultriform process is posterior to the level of the neopalatine in *Pa. solomonis*, *C. guentheri*, *B. trossulus*, and *B. vertebralis* whereas it lies at the level of the neopalatine in *P. hazelae*, *P. guentheri*, *P. dorsalis*, *Pl. solomonis*, *D. bufoniformis*, and *I. mariae*. The cultriform process is longest in *P. guppyi* in which it extends anterior to the neopalatine.

The sphenethmoid is relatively longer in *P. hazelae* and *D. bufoniformis* than it is in the other taxa. The bony posterior margin of the sphenethmoid lies in the posterior part of the orbit of *P. hazelae* and *D. bufoniformis*, but at the midlevel of the orbit in *P. guppyi*, *Pl. solomonis*, *P. dorsalis*, *P. guentheri*, *C. guentheri*, *B. trossulus*, *B. vertebralis*, and *Pa. solomonis*. The bony sphenethmoid is the shortest on *I. mariae*, in which it terminates at the anterior level of the orbit.

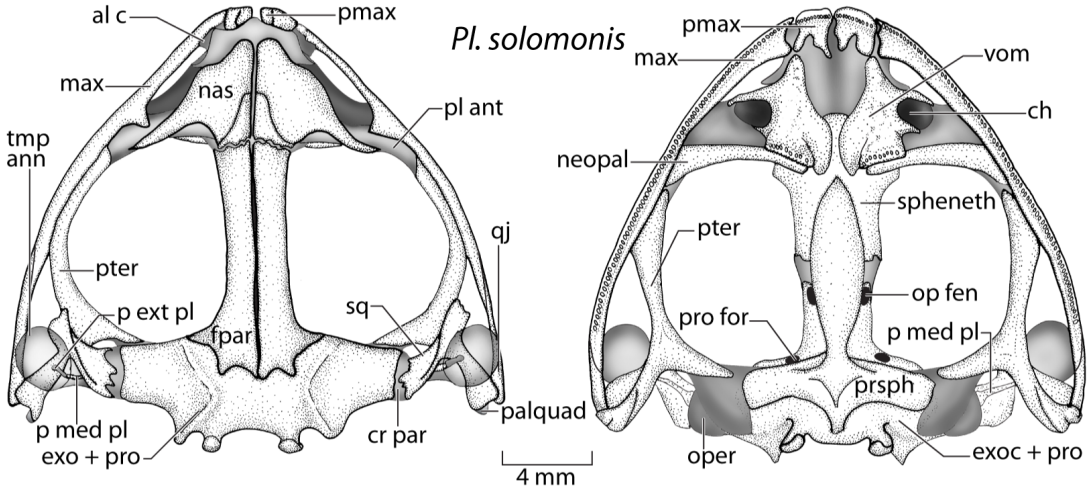

FIG. 8.—Crania: *Platymantis solomonis* (KU 307121) in dorsal (left) and ventral (right) aspects. Black and white stipple represents bone, gray tone is cartilage, and stippling in gray represents mineralization of the cartilage. Abbreviations as in Figure 5.

The cartilaginous separation between sphenethmoid and prootic is broad in *P. dorsalis, P. guentheri*, *Pa. solomonis*, *I. mariae*, *B. trossulus*, and *B. vertebralis* (and most widely separated for *I. mariae*) whereas this separation is moderately narrow in *P. guppyi*, *Pl. solomonis*, *P. hazelae*, and *D. bufoniformis*. The sphenethmoid and prootic are fused for *C. guentheri*.

The exoccipitals are fused to the prootics in all taxa. The epiotic eminences are prominent, and the angle between the two arms of the eminences is approximately 90°. The anterior eminences are slightly longer than the posterior eminences.

Platymantis dorsalis, *Pl. solomonis*, and *C. guentheri* have more ossified otic capsules (exoccipitals synostotically united) than do the remaining taxa. The exoccipitals are united only ventromedially in *P. hazelae* with the exoccipitals dorsomedially separated by an area of mineralization. In *P. guppyi*, *Pa. solomonis*, *B. vertebralis*, *B. trossulus*, *I. mariae*, and *D. bufoniformis*, the exoccipital has areas of mineralization dorso- and ventromedially. All species, except *C. guentheri*, have a cartilaginous crista parotica and a cartilaginous operculum. In *C.*

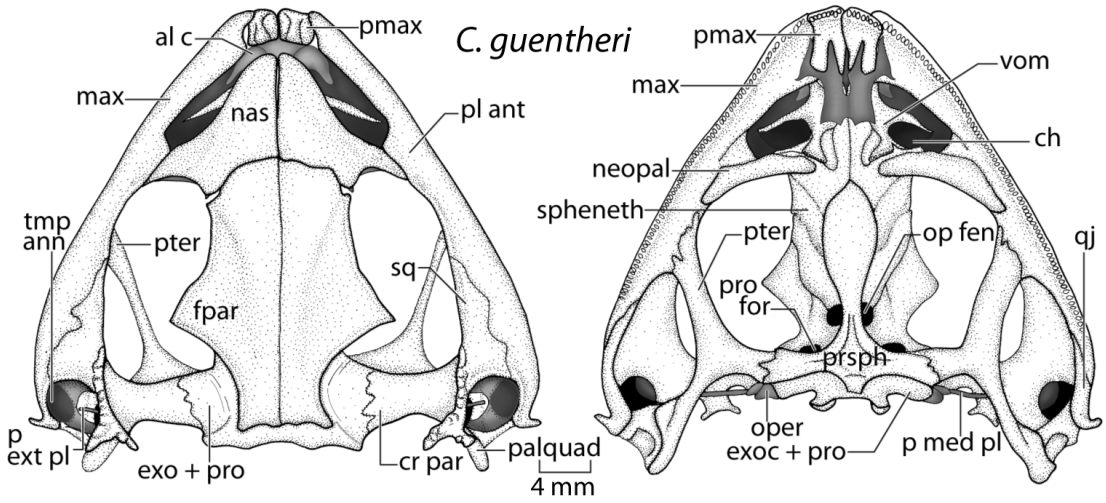

FIG. 9.—Crania: *Ceratobatrachus guentheri* (KU 98467) in dorsal (left) and ventral (right) aspects. Black and white stipple represents bone, gray tone is cartilage, and stippling in gray represents mineralization of the cartilage. Abbreviations as in Figure 5.

guentheri, the entire crista parotica is ossified. In *D. bufoniformis*, the lateral cartilaginous margin of the crista is thinner and mineralized, whereas in the remaining taxa, this cartilage is more extensive and not mineralized.

The pars media plectri is a long, slender, ossified element that extends anterolaterally beneath the crista parotica to terminate in the long, slender cartilaginous pars externa plectri located in the middle of the tympanic annulus for all species.

Dorsal investing bones (Figs. 5–15; Table 1).—The nasals are relatively smaller in *P. dorsalis*, *P. guentheri*, *P. hazelae*, and *Pa. solomonis* than in *Pl. solomonis*, *P. guppyi*, *D. bufoniformis*, *I. mariae*, *B. vertebralis*, *B. trossulus*, and *C. guentheri*. The frontoparietal varies among the eleven species. The frontoparietals are most extensive in *C. guentheri* with an otic flange present; the bones terminate on the posterior half of the otic capsules, whereas they only reach to about the middle (slightly anterior or at the level of the junction of the anterior and posterior epiotic eminences) of the otic capsules in the remaining taxa. The anterior margins of

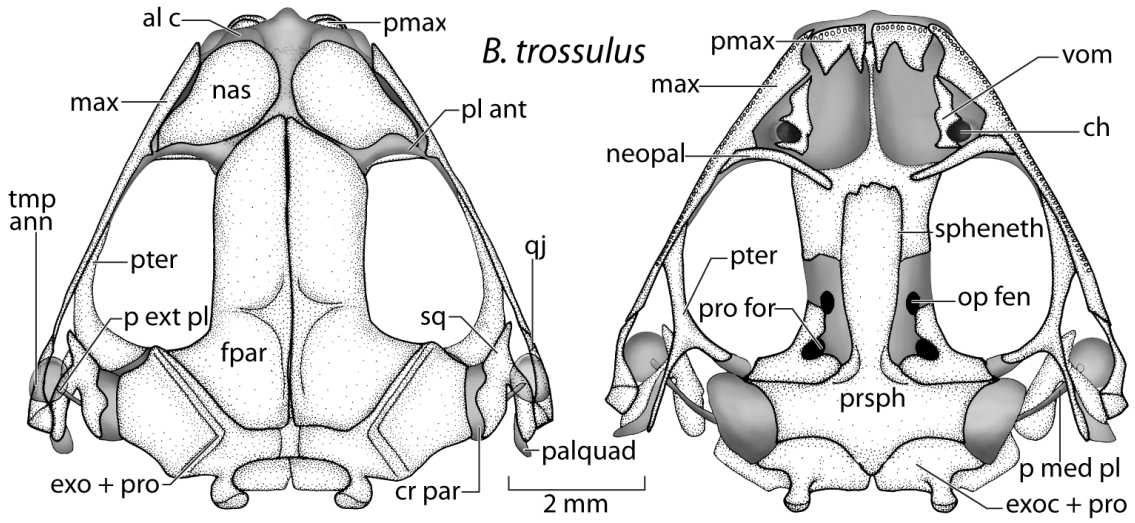

FIG. 10.—Crania: *Batrachylodes trossulus* (KU 145134) in dorsal (left) and ventral (rigtht) aspects. Black and white stipple represents bone, gray tone is cartilage, and stippling in gray represents mineralization of the cartilage. Abbreviations as in Figure 5.

the frontoparietals only are irregular in *P. dorsalis*, *P. guentheri*, *P. guppyi*, *Pl. solomonis*, and *D. bufoniformis*. *Platymantis guppyi* is the only taxa that the anterior margins of are angled in that the anterolateral corner is anterior to that the anteromedial corner. In the other taxa, the anteromedial corner is anterior to the anterolateral. The frontoparietals of *C. guentheri* are expanded to form supraorbital and otic flanges; the bones have a complete medial articulation, whereas they are narrowly separated medially in the remaining species. The frontoparietals completely cover the lateral walls of the braincase from dorsal view in all species.

Ventral investing bones (Figs. 5–15; Table 1).— In *Pl. guppyi*, *Pl. solomonis*, *D. bufoniformis*, and *I. mariae* the parasphenoid overlaps entire length of sphenethmoid, whereas in *P. dorsalis*, *P. guentheri*, *P. hazelae*, *Pa. solomonis*, *B. trossulus*, *B. vertebralis*, and *C. guentheri* the cultriform process overlaps only the posterior half of the bony sphenethmoid. The relationship of the anterior end of the cultriform process of the parasphenmoid with the medial

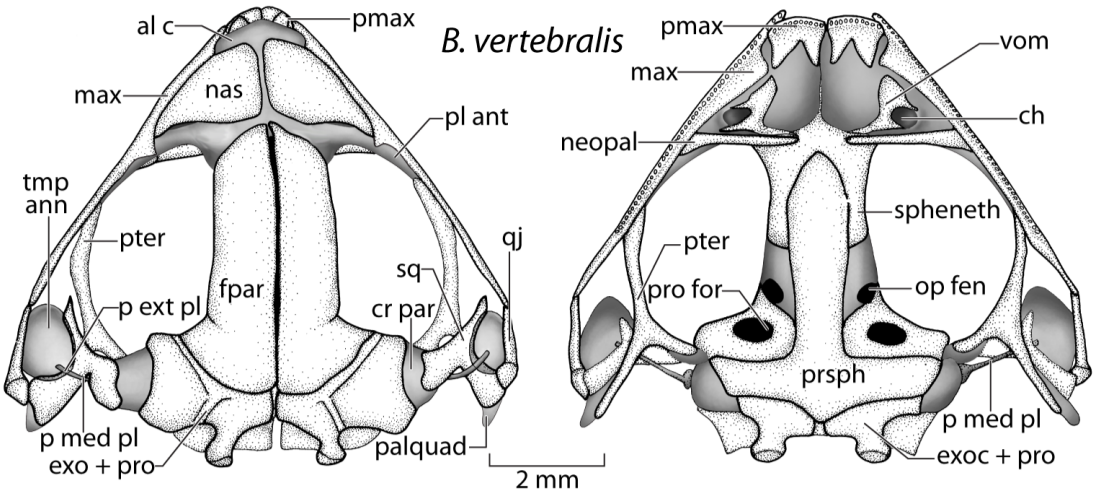

FIG. 11.—Crania: *Batrachylodes vertebralis* (KU 93735) in dorsal (left) and ventral (right) aspects. Black and white stipple represents bone, gray tone is cartilage, and stippling in gray represents mineralization of the cartilage. Abbreviations as in Figure 5.

ends of the neopalatines varies. The anterior tip of the parasphenoid lies anterior to the medial ends of the neopalatines in *Pl. solomonis* and *I. mariae*. It lies between the medial ends of the neopalatines in *C. guentheri*, *P. hazelae*, *P. guppyi*, and *B. vertebralis*, and is posterior to the medial ends of the neopalatines in *D. bufoniformis*, *B. trossulus*, *P. guentheri*, *P. dorsalis*, and *Pa. solomonis*. The cultriform process varies in shape. The lateral margins of the cultriform process converge to an acuminate tip in *C. guentheri*, *P. guppyi*, *Pl. solomonis*, *I. mariae*, *B. vertebralis*, and *D. bufoniformis.* In *P. dorsalis*, *P. hazelae*, *P. guentheri*, *Pa. solomonis* and *B. trossulus,* the cultriform process is irregular and varies from blunt to truncate.

The neopalatine invests the venter of the planum antorbitale, with the medial end overlapping the sphenethmoid in all taxa. In *Ceratobatrachus guentheri*, *Pa. solomonis*, *B. trossulus*, *P. dorsalis*, *P. guentheri*, and *P. guppyi,* the neopalatines are straight, whereas in *D. bufoniformis*, *I. mariae*, *B. vertebralis*, *Pl. solomonis* and *P. hazelae* the medial ends of the neopalatines are angled posterolaterally. In *Platymantis solomonis*, *B. vertebralis*, and *B. trossulus,* the neopalatines articulate with the anterior ramus of the pterygoid, whereas in the

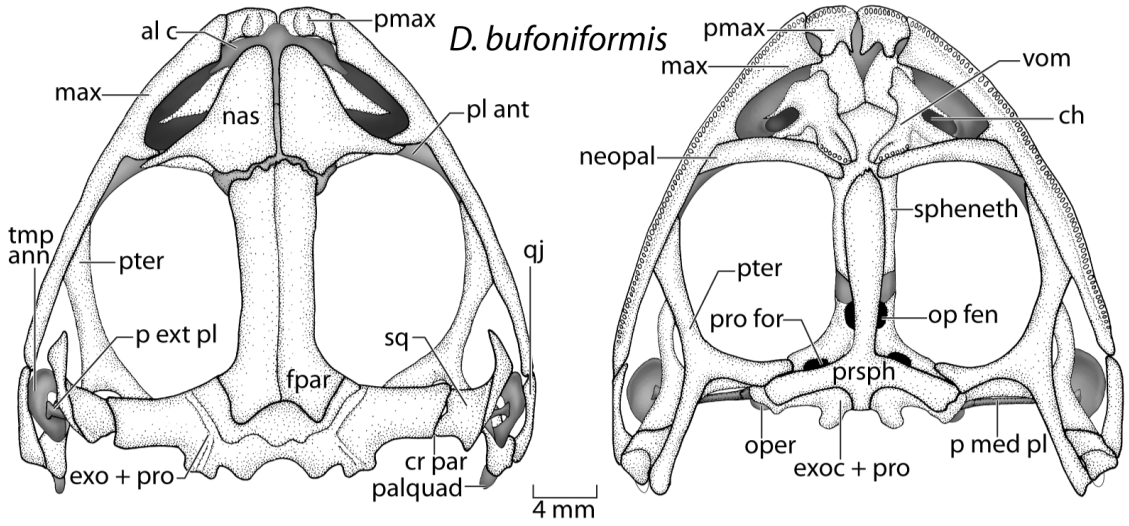

FIG. 12.—Crania: *Discodeles bufoniformis* (KU 307262) in dorsal (left) and ventral (right) aspects. Black and white stipple represents bone, gray tone is cartilage, and stippling in gray represents mineralization of the cartilage. Abbreviations as in Figure 5.

remaining taxa, they do not.

Vomers are present in all taxa. They are relatively larger in *P. guppyi, Pl. solomonis*, *C. guentheri*, and *D. bufoniformis* than they are in the other taxa. Among the latter, the vomers are relatively smaller in *Pa. solomonis*, *B. vertebralis*, and *B. trossulus* than in *P. dorsalis*, *P. guentheri*, *P. hazelae*, and *I. mariae*. *Batrachylodes vertebralis* and *B. trossulus* have vomers that are broadly separated from one another medially. In contrast, *P. dorsalis*, *P. guentheri*, *P. hazelae*, *P. guppyi*, *C. guentheri*, *I. mariae*, *Pa. solomonis*, and *D. bufoniformis* have moderately separated vomers. *Platymantis solomonis* is the only taxon that has vomers with a narrow medial separation. The choana, and prechoanal and postchoanal processes have a uniform morphology in all taxa. The processes are curved, with the prechoanal process supporting half or more of the anterior margin of the choana; the smaller postchoanal process supports the medial margin of the choana. Dentigerous processes are absent or small in *Pa. solomonis*, *B. trossulus*, and *B. vertebralis*. In the other taxa, the base of the dentigerous process lies at the union of the pre- and

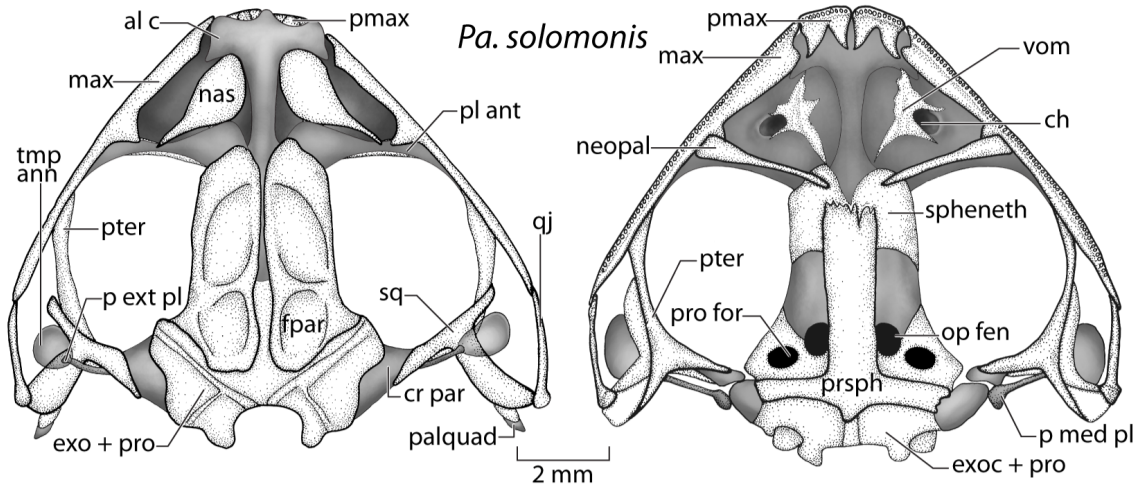

FIG. 13.—Crania: *Palmatorappia solomonis* (KU 93749) in dorsal (left) and ventral (right) aspects. Black and white stipple represents bone, gray tone is cartilage, and stippling in gray represents mineralization of the cartilage. Abbreviations as in Figure 5.

postchoanal processes; a basal flange extends medially from the processes. The dentigerous processes are larger in *P. guppyi*, *Pl. solomonis*, *C. guentheri*, and *D. bufoniformis* than in *P. dorsalis*, *P. hazelae*, *P. guentheri*, and *I. mariae*.

Maxillary arcade (Figs. 5–15; Table 1).—The maxillae and premaxillae are dentate in all species. The pars facialis of the maxilla forming a smooth edge is highest anteriorly. The pars palatina of the premaxilla is moderately developed, and bears medial and lateral processes. The lateral process of the pars palatina of the premaxilla is larger than the medial process in *P. dorsalis*, *P. guentheri*, *P. hazelae*, *Pa. solomonis*, *B. trossulus*, *B. vertebralis*, and *C. guentheri* in contrast to *P. guppyi, Pl. solomonis*, and *D. bufoniformis*, whereas the medial processes are slightly larger than the lateral processes.

In *C. guentheri,* the anterior ends of the pars facialis of the maxillae slightly overlaps the lateral margins of the premaxilla, whereas it does not in the other taxa.

Suspensory apparatus (Figs. 5–15; Table 1).— The pterygoid is slender in all taxa. Although the anterior ramus does not reach the neopalatine in most species, *Pl. solomonis*, *B.*

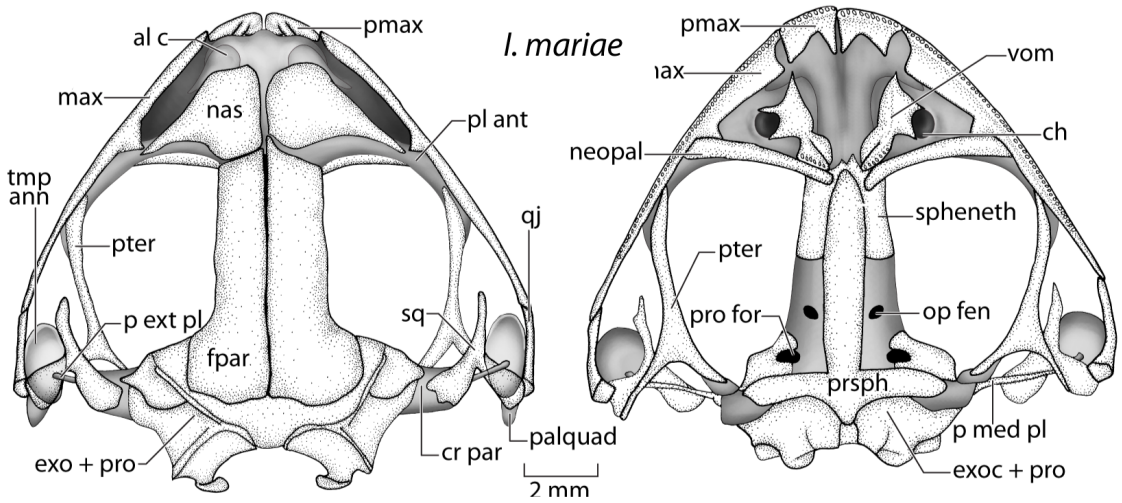

FIG. 14.—Crania: *Ingerana mariae* (KU 309472) in dorsal (left) and ventral (right) aspects. Black and white stipple represents bone, gray tone is cartilage, and stippling in gray represents mineralization of the cartilage. Abbreviations as in Figure 5.

vertebralis, and *B. trossulus* have longer anterior rami that articulate with the neopalatines. In all taxa except *C. guentheri,* the anterior pterygoid ramus is longer than the medial and lateral rami. *Ceratobatrachus guentheri* has a relatively short anterior ramus, which is equal in length to the lateral and medial rami, has the anterior end fused to the maxillary, and the medial ramus fused with the ventral margin of the exoccipital. In *D. bufoniformis*, the medial ramus invests in the ventral margin of the exocciptals. In *Pl. solomonis*, *P. guentheri*, *P. hazelae*, *P. dorsalis*, *P. guppyi*, *Pa. solomonis*, *I. mariae*, *B. trossulus*, and *B. vertebralis* the medial ramus invests in the ventral margin of the cartilaginous crista parotica.

The T-shaped squamosal has an otic ramus that is longer and more expanded longer than the zygomatic ramus in *P. dorsalis*, *P. guentheri*, *P. hazelae*, *Pl. solomonis*, *P. guppyi*, *B. trossulus*, *B. vertebralis*, *Pa. solomonis*, and *I. mariae*. The head of the squamosal is more symmetrical in *D. bufoniformis*, with the otic ramus and the zygomatic ramus equal in length and expansion. In *C. guentheri*, the squamosal differs and notably, having an otic ramus that is

shorter than the zygomatic ramus. The posterior end of the otic ramus is bifurcated and fused to the exoccipital with visible sutures. The zygomatic ramus highly expanded distally. The otic ramus articulates the dorsolateral margin of the crista parotica in *P. dorsalis*, *P. guentheri*, *P. hazelae*, *Pl. solomonis*, *P. guppyi*, *B. trossulus*, *B. vertebralis*, *Pa. solomonis* and *I. mariae*, whereas the otic ramus articulates with the dorsolateral margin of the exoccipital in *D. bufoniformis*. In all taxa, the ventral ramus is longer than both the otic and zygomatic rami; it invests in the palatoquadrate and articulates with the quadratojugal.

TABLE 1.—Summary of distribution of cranial characters among Ceratobatrachine taxa (+ present, – absent). A, *Platymantis guentheri*; B, *Platymantis hazelae*; C, *Platymantis dorsalis*; D, *Platymantis solomonis*; E, *Platymantis guppyi*; F, *Batrachylodes vertebralis*; G, *Batrachylodes trossulus*; H, *Palmatorappia solomonis*; I, *Ceratobatrachus guentheri*; J, *Discodeles bufoniformis*; K, *Ingerana mariae*.

Character	Taxon										
	A	B	C	D	E	F	G	H	I	J	K
Cranial Shape & Proportion											
Greatest skull width at quadratojugal-maxilla articulation	+	+	+	+	+	+	+	+	+	+	+
Skull less than 15% wider than long	+	–	+	+	+	+	–	–	–	–	–
Frontoparietals posterior margin greatest skull height	+	+	+	+	+	+	+	+	+	+	+
Greatest skull height < 35% of premaxilla-quadratojugal length	–	–	–	–	+	–	–	–	–	+	–
Rostrum > 35% of premaxilla-quadratojugal length	–	+	+	+	+	–	–	–	+	–	+
Rostrum < 35% of medial skull length	–	–	–	–	–	+	+	–	–	–	–
Midorbital braincase width < 25% of medial skull length	–	–	–	+	–	–	–	–	–	+	–
Sphenethmoid											
Broad separation between sphenethmoid & prootic	+	–	+	–	–	+	+	+	–[1]	–	+
Posterior margin of sphenethmoid ends at midorbit	+	–	+	+	+	+	+	+	+	–	–
Posterior margin of sphenethmoid ends posterior of midorbit	–	+	–	–	–	–	–	–	–	+	–
Posterior margin of sphenethmoid ends anterior of midorbit	–	–	–	–	–	–	–	–	–	–	+
Sphenethmoid & prootic fused	–	–	–	–	–	–	–	–	+	–	–
Prootic											
Exoccipitals fused to prootic	+	+	+	+	+	+	+	+	+	+	+
Anterior & posterior epiotic eminences vertex ~90°	+	+	+	+	+	+	+	+	+	+	+
Anterior eminence slightly longer than posterior eminence	+	+	+	+	+	+	+	+	+	+	+

Otic capsules synostotically united	–	+[2]	+	+	–	–	–	–	+	–	–
Crista Parotica											
Pars externa plectri cartilaginous	+	+	+	+	+	+	+	+	+	+	+
Pars media plectri long, slender, ossified	+	+	+	+	+	+	+	+	+	+	+
Nasals											
Medial margins broadly separated (vs. moderately or narrowly)	–	+	–	–	–	–	–	+	–[3]	–	–
Medial margins parallel (vs. posteriorly divergent)	+	–	–	–	–	–	–	–	–	–	–
Anterodistal margins notched	+	–	–	+	–	–	–	–	–	–	–
Nasals relatively small	+	+	+	–	–	–	–	+	–	–	–
Nasals moderately separated from frontoparietals	+	+	+	–	+	–	–	–	–	–	–
Nasals narrowly separated from frontoparietals	–	–	–	+	–	+	+	–	+	+	+
Nasals broadly separated from frontoparietals	–	–	–	–	–	–	–	+	–	–	–
Anteromedial prenasal process present	+	+	+	+	+	+	+	+	+	+	+
Internasal septum terminates into median prenasal process	+	+	+	+	+	+	+	+	+	+	+
Plana antorbitalae cartilaginous (vs. ossified)	+	+	+	+	+	+	+	+	–	+	+
Neopalatines											
Parasphenoid margin level with medial ends of neopalatines	+	+	+	+	–	–	–	–	–	+	+
Parasphenoid margin posterior to medial ends of neopalatines	–	–	–	–	–	+	+	+	+	–	–
Parasphenoid margin anterior to medial ends of neopalatines	–	–	–	–	+	–	–	–	–	–	–
Medial ends of neopalatines overlap sphenthmoid	+	+	+	+	+	+	+	+	+	+	+
Neopalatine lateral ends separated from pterygoid	+	+	+	–	+	–	–	+	+	+	+
Neopalatine with straight shaft	+	–	+	–	+	–	+	+	+	–	–
Vomers											

Dentigerous process present	+	+	+	+	+	–	–	–	+	+	+
Vomers relatively large	–	–	–	+	+	–	–	–	+	+	–
Postchoanal process smaller than prechoanal process	+	+	+	+	+	+	+	+	+	+	+
Vomers with broad medial separation	–	–	–	–	–	+	+	–	–	–	–
Vomers with moderate medial separation	+	+	+	–	+	–	–	+	+	+	+
Vomers with narrow medial separation	–	–	–	+	–	–	–	–	–	–	–
Curved boney processes border half or over half choana	+	+	+	+	+	+	+	+	+	+	+
Pterygoid											
Anterior ramus reaches neopalatine	–	–	–	+	–	+	+	–	–	–	–
Medial ramus invests ventral margin of crista parotica	+	+	+	+	+	+	+	+	+	–	+
Anterior ramus longer than medial & posterior rami	+	+	+	+	+	+	+	+	–	+	+
Anterior ramus equal in length to medial & posterior rami	–	–	–	–	–	–	–	–	+	–	–
Squamosal											
Otic ramus longer & more expanded than zygomatic ramus	+	+	+	+	+	+	+	+	–	–	+
Otic ramus shorter & less expanded than zygomatic ramus	–	–	–	–	–	–	–	–	+	–	–
Otic ramus equal in length & expansion to zygomatic ramus	–	–	–	–	–	–	–	–	–	+	–
Ventral ramus longer than otic & zygomatic rami	+	+	+	+	+	+	+	+	+	+	+
Otic ramus articulates with crista parotica	+	+	+	+	+	+	+	+	–	–	+
Maxillary Arcade											
Premaxillae & maxillae dentate	+	+	+	+	+	+	+	+	+	+	+
Pars facialis anterior ends overlap premaxillae lateral margins	–	–	–	–	–	–	–	–	+	–	–
Pars palatina medial process smaller than lateral process	+	+	+	–	–	+	+	+	+	–	–
Alary cartilage visible in dorsal view	+	+	+	+	+	+	+	+	+	+	+

Frontoparietals											
Extend approximately to middle of otic capsules	+	+	+	+	+	+	+	+	–	+	+
End anterior to or level with epiotic eminences vertex	+	+	+	+	+	+	+	+	–	+	+
Anterior margins irregularly scalloped	+	–	+	+	+	–	–	–	–	+	–
Anteromedial margins angled to extend more anterior	+	–	+	+	–	–	–	–	+	+	–
Otic flange of frontoparietal present	–	–	–	–	–	–	–	–	+	–	–
Narrow medial separation (vs. complete articulation)	+	+	+	+	+	+	+	+	–	+	+
Parasphenoid											
Cultriform process margin aligns with neopalatine medial ends	–	+	–	–	+	+	–	–	+	–	–
Cultriform process margin anterior to neopalatine medial ends	–	–	–	+	–	–	–	–	–	–	+
Cultriform process margin posterior to neopalatine medial ends	+	–	+	–	–	–	+	+	–	+	–
Cultriform process lateral margins converge to acuminate tip	–	–	–	+	+	+	–	–	+	+	+

[1] Sphenethmoid & prootic are fused
[2] Exoccipitals united only ventromedially
[3] Medial walls of the nasal capsules abut

Postcranial Osteology

Vertebral column (Fig. 16 and Fig. 17; Table 2).—There are eight, non-imbricate presacral vertebrae each species. The pattern of neural spines, based on size and presence, on the different presacral vertebrae greatly varies among the eleven taxa. Overall, *Platymantis dorsalis, Pl. solomonis*, *C. guentheri*, *B. vertebralis*, and *D. bufoniformis* have larger, more distinct neural spines than the other six taxa.

Platymantis dorsalis has neural spines with rounded medial processes on the posterior margin on Presacrals II–VI (with the process extending to the anterior end on Presacral II). On *P. dorsalis*, the neural spines of Presacrals II and III are larger than the neural spines of Presacrals IV–VI (size of neural spine of Presacral IV > size of neural spines of Presacrals II and III). *Platymantis solomonis* has Presacrals II–V bearing neural spines with medial processes on posterior margins (with them being very distinct on Presacrals II and III) and small, reduced neural spine present on Presacral VI. *Ceratobatrachus guentheri* has neural spines on Presacrals II–VII with rounded posterior margin processes. On Presacral II, the process is modified to a triangle-shape, extending to the anterior end. The processes on the neural spines are smaller on Presacrals V–VII than on Presacrals II–IV on *C. guentheri*. *Discodeles bufoniformis* has neural spines with medial processes on the posterior margins on Presacrals II–VII (size of neural spines largest on Presacrals II and III). *Batrachylodes vertebralis* has neural spines with medial processes on the posterior margin on Presacrals II–IV (size of neural spines of Presacral IV < size of neural spines of Presacral II and III).

Ingerana mariae has one reduced neural spine on the posterior margin of Presacral II. Neural spines are absent on all presacral vertebrae for *Pa. solomonis* (with the exception of a very reduced process on the anterior margin of Presacral II). Presacrals II– VIII have neural

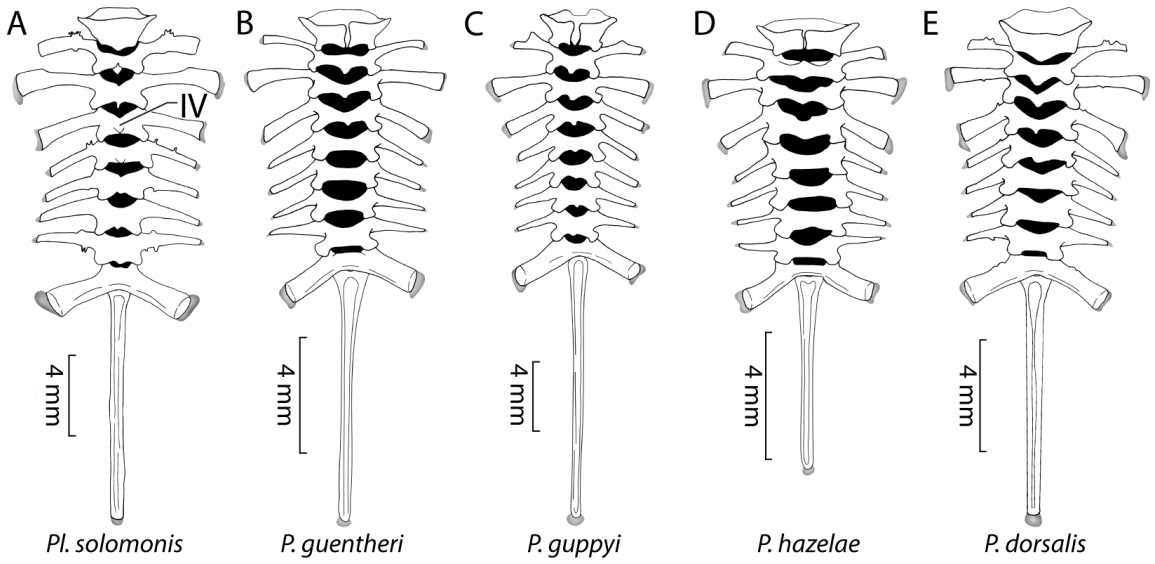

FIG. 15.—Vertebral columns in dorsal view: A, *Platymantis solomonis* (KU 307121). B, *Platymantis guentheri* (KU 319619). C, *Platymantis guppyi* (KU 98161). D, *Platymantis hazelae* (KU 306739). E, *Platymantis dorsalis* (KU 313709). Bone shown in white and cartilage in gray.

spines with medial processes on the posterior margins (size of neural spines of Presacrals II–IV > size of neural spines of Presacrals V–VIII) on *P. guppyi*. *Platymantis hazelae* has neural spines with medial processes on Presacrals II and III on both the anterior and posterior margins (with it being more defined in Presacral II) and a small, reduced neural spine present on the posterior margin on Presacral IV. *Batrachylodes trossulus* has neural spines with medial processes on Presacrals II and III on the posterior margins, with a very reduced process on Presacral IV. *Platymantis guentheri* has Presacrals II–IV with neural spines with medial processes on the posterior margins (medial process also on the anterior margin for Presacral II).

A notch is present on Presacral II transverse processes on *P. guppyi*, *C. guentheri*, and *D. bufoniformis* and on Presacrals II and III transverse processes on *Pl. solomonis*. The transverse processes of Presacrals II through IV are slightly more robust than those on the posterior presacrals in *P. dorsalis*, *P. guentheri*, *P. hazelae*, *P. guppyi*, *Pl. solomonis*, *B. trossulus*, *B. vertebralis*, *C. guentheri*, and *D. bufoniformis*, with the transverse processes of Presacrals IV

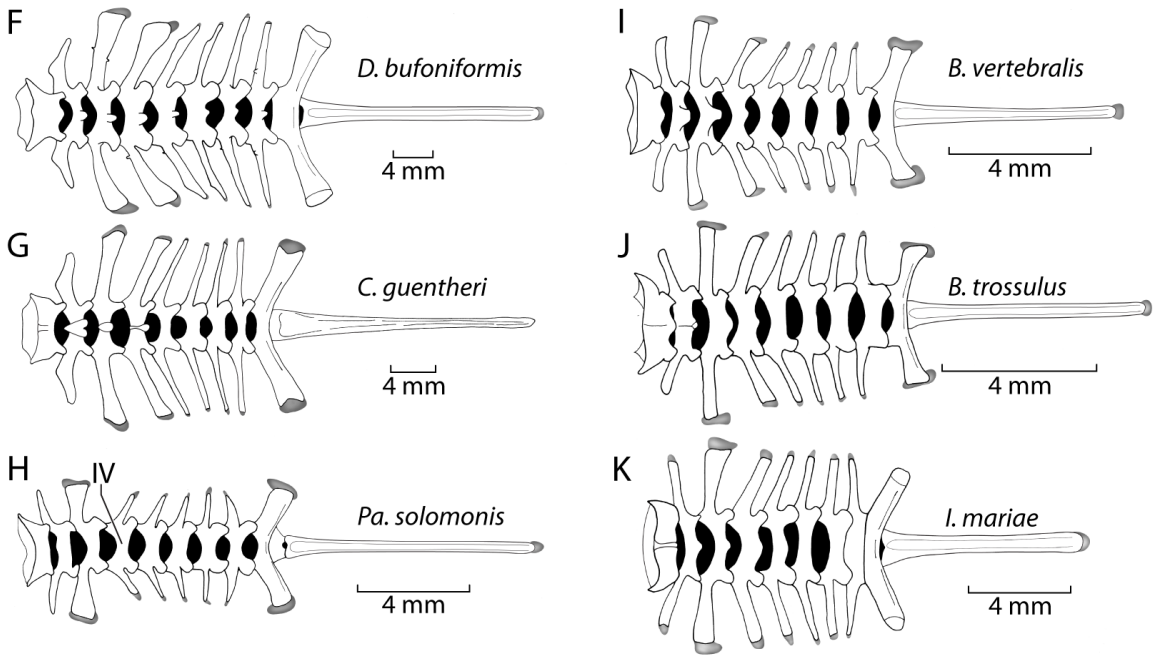

FIG. 16.—Vertebral columns in dorsal view: F, *Discodeles bufoniformis* (KU 307262). G, *Ceratobatrachus guentheri* (KU 98467). H, *Palmatorappia solomonis* (KU 93749). I, *B. vertebralis* (KU 93735). J, *Batrachylodes trossulus* (KU 145134). K, *Ingerana mariae* (KU 309472). Bone shown in white and cartilage in gray.

only slightly more robust than the posterior transverses processes. Irregular, small spurs are present on along the anterior and posterior margins on some of the transverse processes on only *Pl. solomonis*, *P. dorsalis* and *D. bufoniformis*.

The vertebral profile varies significantly among the taxa. The width of the sacral diapophyses in *Platymantis guentheri*, *P. hazelae*, *P. dorsalis*, and *I. mariae* is narrower than all the presacral transverse processes. The sacrum is equal in width to the narrowest transverse processes in *Pl. solomonis*, *B. vertebralis*, and *B. trossulus*. *Platymantis guppyi*, *Pa. solomonis*, *C. guentheri*, and *D. bufoniformis* have one or more transverse processes that are narrower than the sacrum.

The vertebral profiles in decreasing order of overall width of the bony parts are as follow: III > IV = VIII > II = V = VI = VII > sacrum for *P. guentheri*; III > IV > II = V = VI = VII =

VIII > sacrum for *P. dorsalis*; III > IV = VIII > II = V = VI = VII = sacrum for *Pl. solomonis*; III > II = IV > V = VI = VII = VIII > sacrum for *P. hazelae*; III > IV = sacrum > V = VI = VII = VIII > II for *C. guentheri*; III = IV = V = VI = VII > VIII > II > sacrum for *I. mariae*; III = sacrum > II = IV = V = VI = VII = VIII for *Pa. solomonis*; III > IV > V = VI = VII = VIII = II = sacrum for *B. vertebralis*; III > IV = V = VI = VII = VIII > II = sacrum for *B. trossulus*; III > IV = VIII = sacrum > V = VI = VII = II for *P. guppyi*; III > VII = VIII = sacrum > VI > V > IV > II for *D. bufoniformis*.

The orientation of the transverse processes for the presacral vertebrae varies among the eleven taxa. The bony sacral diapophysis is not broadly expanded, and is oriented posterolaterally for all eleven species. *Platymantis guentheri*, *D. bufoniformis*, *Pl. solomonis*, *P. guppyi*, and *C. guentheri* have transverse processes with only posterolateral or lateral orientations. The orientation of the transverse processes is lateral for Presacrals II, III and VIII, posterolateral for Presacrals IV–VI and sacrum, and posterolateral to lateral for Presacral VII on both *P. guentheri* and *D. bufoniformis*. The orientation of the transverse processes is lateral for Presacrals II and III, posterolateral for Presacrals IV–VII and sacrum, and posterolateral to lateral for Presacral VIII on both *Pl. solomonis* and *P. guppyi*. *Ceratobatrachus guentheri* has transverse processes with lateral orientation for Presacrals II and III, posterolateral for Presacral IV–VII and sacrum, and posterolateral to lateral for Presacral VIII.

Anterolateral orientations can be found in some of the transverse processes of *P. dorsalis*, *P. hazelae*, *I. mariae*, *Pa. solomonis*, *B. vertebralis*, and *B. trossulus*. The orientation of the transverse processes is lateral for Presacral III and VIII, lateral to anterolateral for Presacral II, posterolateral for Presacrals IV, V, VI and sacrum, and posterolateal to lateral for Presacral VII for *P. dorsalis*. The orientation of the transverse processes is anterolateral for Presacral II, lateral

to anterolateral for Presacral III and VIII, posterolateral for Presacrals IV, V, VI and sacrum, and posterolateral to lateral for Presacral VII on *P. hazelae*. The orientation of the transverse processes is anterolateral for Presacral II and VIII, lateral for Presacrals III and VII, posterolateral for Presacral IV, V, VI and sacrum on *I. mariae* and *Pa. solomonis*. The orientation of the transverse processes is anterolateral for Presacral II, lateral for Presacrals III and VIII, posterolateral for Presacrals IV, V, VI, VII and sacrum on *B. vertebralis*. The orientation of the transverse processes is anterolateral for Presacral II, lateral for Presacrals III and VIII, posterolateral for Presacral IV, V, VI and sacrum, and posterolateral to lateral for Presacral VII on *B. trossulus*.

The urostyle is longer than the length of the presacral portion of the vertebral column (medial length of Presacral I through sacrum) in only *P. guppyi*; it is equal to the length of the presacral portion of the vertebral column in *B. vertebralis* and *Pa. solomonis*. The urostyle is slightly shorter than the length of the presacral portion of the vertebral column in *C. guentheri*, *I. mariae* and *P. guentheri*, whereas the urostyle is moderately shorter than the length of the presacral portion of the vertebral column in *P. hazelae*, *B. trossulus*, *P. dorsalis*, *Pl. solomonis* and *D. bufoniformis*. The urostyle has a bicondylar articulation with the sacrum and bears a dorsal crest throughout most of its length in all taxa. The anterior end of the dorsal crest is bifurcate in *P. hazelae*.

Pectoral girdle (Fig. 18 and Fig. 19; Table 2).— The prezonal elements include omosternum with a fan-shaped cartilage plate and bifurcate bony style in all species. The distal ramus of the omosternum is slightly expanded on the anterior end on *P. guppyi*, *P. dorsalis*, and *I. mariae*. The distal ramus of the omosternum is not expanded on the anterior end on *P. hazelae*, *Pl. solomonis*, *P. guentheri*, *C. guentheri*, *Pa. solomonis*, *D. bufoniformis*, *B. trossulus* and *B.*

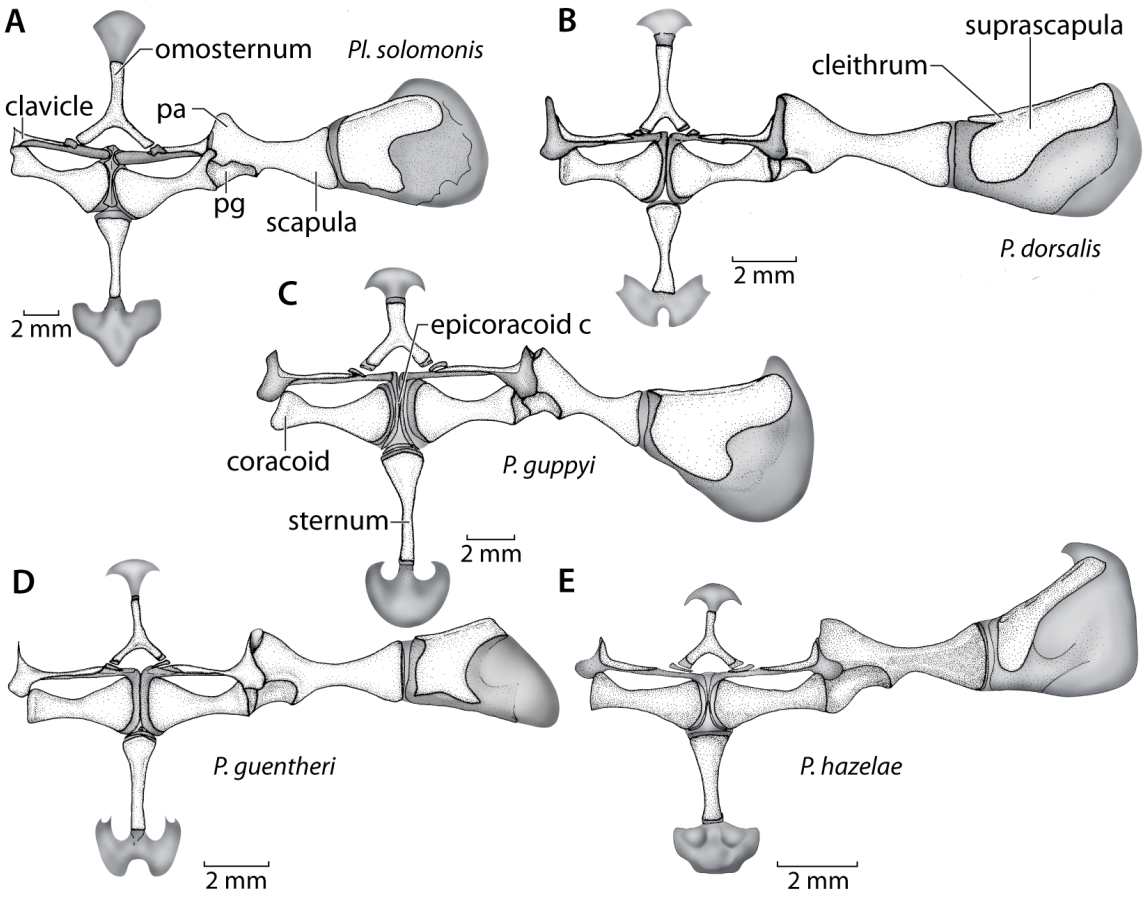

FIG. 17.—Pectoral girdles in ventral view: A, *Platymantis solomonis* (KU 307121). B, *P. dorsalis* (KU 313709). C, *P. guppyi* (KU 98161). D, *P. guentheri* (KU 319619). E, *P. hazelae* (KU 306739). The left scapula and suprascapula have been deflected into the ventral plane for the purposes of illustration. Black and white stipple represents bone, gray tone is cartilage, and stippling in gray represents mineralization of the cartilage.

vertebralis. The distal ramus of the omosternum is moderately longer than the medial rami of the omosternum in *P. dorsalis* and *I. mariae*, whereas it is slightly longer than the medial rami of the omosternum in *Pl. solomonis*, *C. guentheri*, *B. trossulus*, *B. vertebralis*, *P. guppyi*, and *D. bufoniformis.* The distal ramus of the omosternum is the same length as the medial rami in *P. hazelae*, *Pa. solomonis*, and *P. guentheri*. The sternum is wider anteriorly in all species except *B. trossulus*.

A fan-shaped cartilage plate is present on the sternum in all eleven species. The sternum is

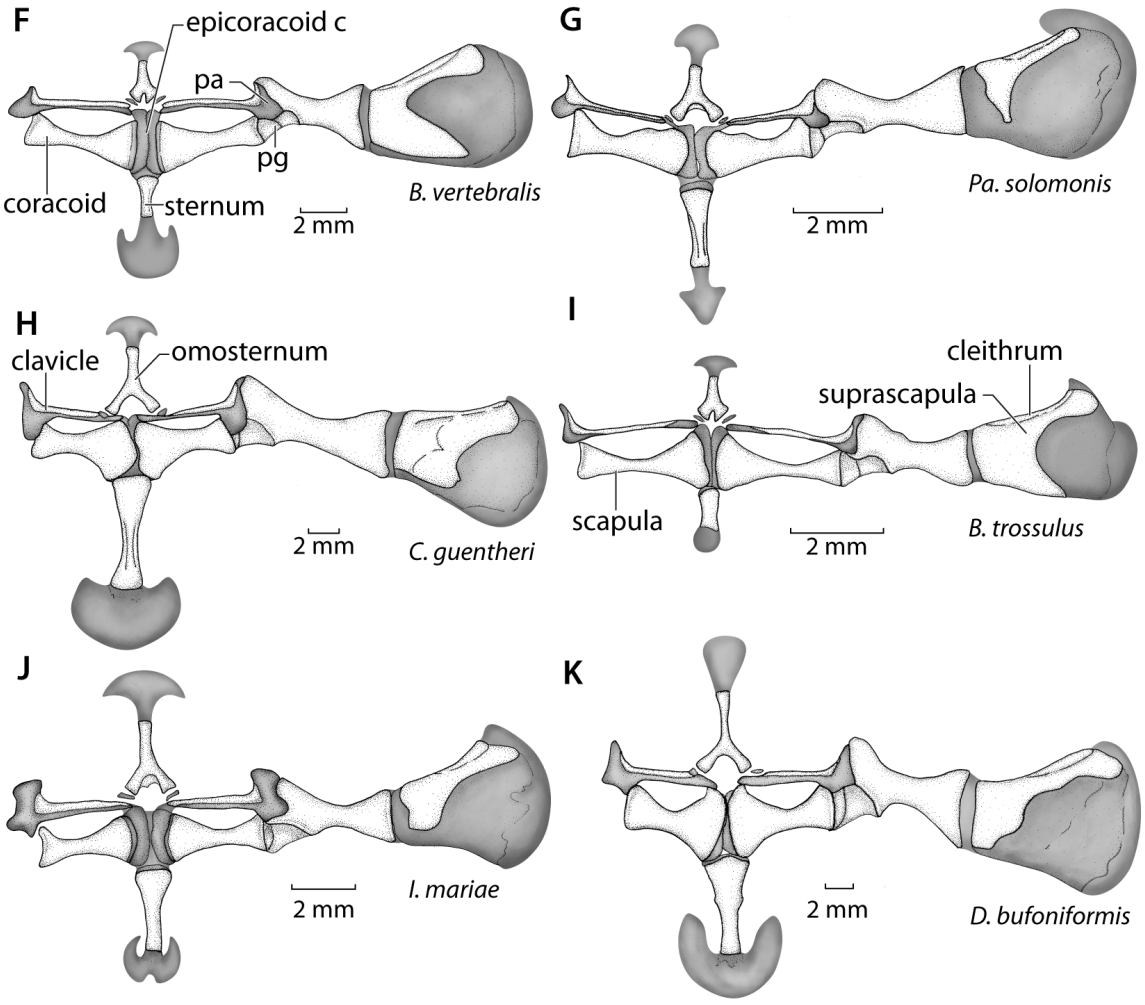

FIG. 18.—Pectoral girdles in ventral view: F, *Batrachylodes vertebralis* (KU 93735). G, *Palmatorappia solomonis* (KU 93749). H, *Ceratobatrachus guentheri* (KU 98467). I, *B. trossulus* (KU 145134). J, *Ingerana mariae* (KU 309472). K, *Discodeles bufoniformis* (KU 307262). The left scapula and suprascapula have been deflected into the ventral plane for the purposes of illustration. Black and white stipple represents bone, gray tone is cartilage, and stippling in gray represents mineralization of the cartilage.

wider on the anterior end in all species except *B. trossulus*.

The zonal portion of the pectoral girdle is moderately long, with the medial length being slightly less than the width of the girdle between the glenoid fossae in *B. vertebralis*, *Pa. solomonis*, *P. hazelae*, *P. guentheri* and *I. mariae*, and greater than the width of the girdle between the glenoid fossae in *P. dorsalis*, *P. guppyi*, *Pl. solomonis*, *D. bufoniformis*, and *C. guentheri*. The clavicles have a lateral orientation, with the medial tips visibly separated from

one another and visible procoracoid in background in *P. guppyi*, *P. guentheri*, *P. dorsalis*, *Pl. solomonis*, *B. trossulus*, *B. vertebralis*, *C. guentheri*, *I. mariae*, and *D. bufoniformis*, whereas the clavicles of *P. hazelae* and *Pa. solomonis* have a posteromedial orientation. The shaft of clavicle is straight and visibly separate from base of omosternum in all species.

The coracoid is well developed in all taxa. The coracoid is the most robust in *Pa. solomonis* and *B. vertebralis,* in which the midshaft width is about 25% the length of the coracoid (midshaft width roughly 14–20% for the remaining taxa). *Platymantis solomonis*, *C. guentheri*, *D. bufoniformis*, and *P. guppyi* have coracoids with the most highly expanded sternal end; in these, the midshaft width is about 30% (27–25%) of the width of the expansion of the sternal end of the bone. The midshaft width is between 30% and 45% of the width of the sternal end expansion of the coracoid for *P. dorsalis*, *P. hazelae*, *I. mariae*, *B. trossulus*, and *P. guentheri*. For the two taxa that have the stoutest coracoids (*Pa. solomonis* and *B. vertebralis*), the midshaft width is respectively 48% and 57% of the width of the expansion of the sternal end of the coracoid.

The pectoral fenestra is triangular in all taxa and is narrowest in *P. guentheri* and *B. trossulus*. The pectoral fenestra more than two times as wide as it is high in *D. bufoniformis*, *Pa. solomonis*, *I. mariae* and *B. vertebralis*, more than three times as wide as it is high in *C. guentheri*, *P. hazelae*, *P. dorsalis*, *Pl. solomonis* and *P. guppyi*, and more than four times wide as it is high in *P. guentheri* and *B. trossulus*.

The scapula is long with equal-sized partes acromialis and glenoidalis in *P. guentheri*, *P. hazelae*, *D. bufoniformis*, and *C. guentheri*. The pars acromialis is slightly larger than the pars glenoidalis in *P. dorsalis*, *Pl. solomonis*, *I. mariae*, *Pa. solomonis*, *B. trossulus*, *B. vertebralis*, and *P. guppyi*. The scapula is somewhat longer than the clavicle in *P. hazelae*, *P. dorsalis*, and

C. guentheri (clavicle length less than 65% scapula length). The scapula is slightly longer than the clavicle in *I. mariae*, *Pl. solomonis*, *D. bufoniformis*, *Pa. solomonis*, and *P. guentheri*, and shorter than the calvicle in *B. trossulus*, *P. guppyi*, and *B. vertebralis*.

The suprascapula is the least ossified in *P. hazelae* (about 30% ossified), moderately ossified (50–80%) in *B. vertebralis*, *I. mariae*, *B. trossulus*, *P. guentheri*, *C. guentheri*, *Pa. solomonis*, and *Pl. solomonis*, and highly ossified (90–95% ossified) for *P. guppyi*, *P. dorsalis* and *D. bufoniformis*. The cleithrum is a slender bone along the leading edge of the suprascapular blade.

Pelvic girdle (Fig. 20 and Fig. 21; Table 2).— Dorsolateral crests are present on the ilial shafts of all species. The ilial shafts are long and slender in *P. guppyi*, *P. hazelae*, *P. guentheri*, *B. trossulus*, *B. vertebralis*, *Pa. solomonis*, and *C. guentheri*, whereas *Pl. solomonis*, *P. dorsalis*, *I. mariae*, and *D. bufoniformis* have more robust shafts. The ilial prominence is lower than the anterodorsal margins of the ilial shafts in all species.

Platymantis solomonis, *P. dorsalis*, *C. guentheri* and *D. bufoniformis* have a completely ossified pubis, whereas the pubes of *P. guentheri*, *P. hazelae*, *P. guppyi*, *B. vertebralis*, *B. trossulus*, *I. mariae*, and *Pa. solomonis* are mineralized. The preacetabular angle is less than 90° in *C. guentheri*, *D. bufoniformis*, *B. vertebralis*, *P. hazelae*, and *Pl. solomonis*, whereas it is equal to or slightly greater than 90° in *I. mariae*, *Pa. solomonis*, *P. guppyi*, and *B. trossulus*.

Platymantis solomonis and *C. guentheri* are the only two taxa that completely lack a fenestra in the acetabulum owing to hyperossification. Sutures on the fused acetabulum are visible in *C. guentheri,* but not in *Pl. solomonis*. *Batrachylodes trossulus* has a round, fused acetabulum with visible sutures and mineralized cartilage in place of a fenestra at the center of the acetabulum. The acetabulum is fused with visible sutures and a triangular fenestra in the

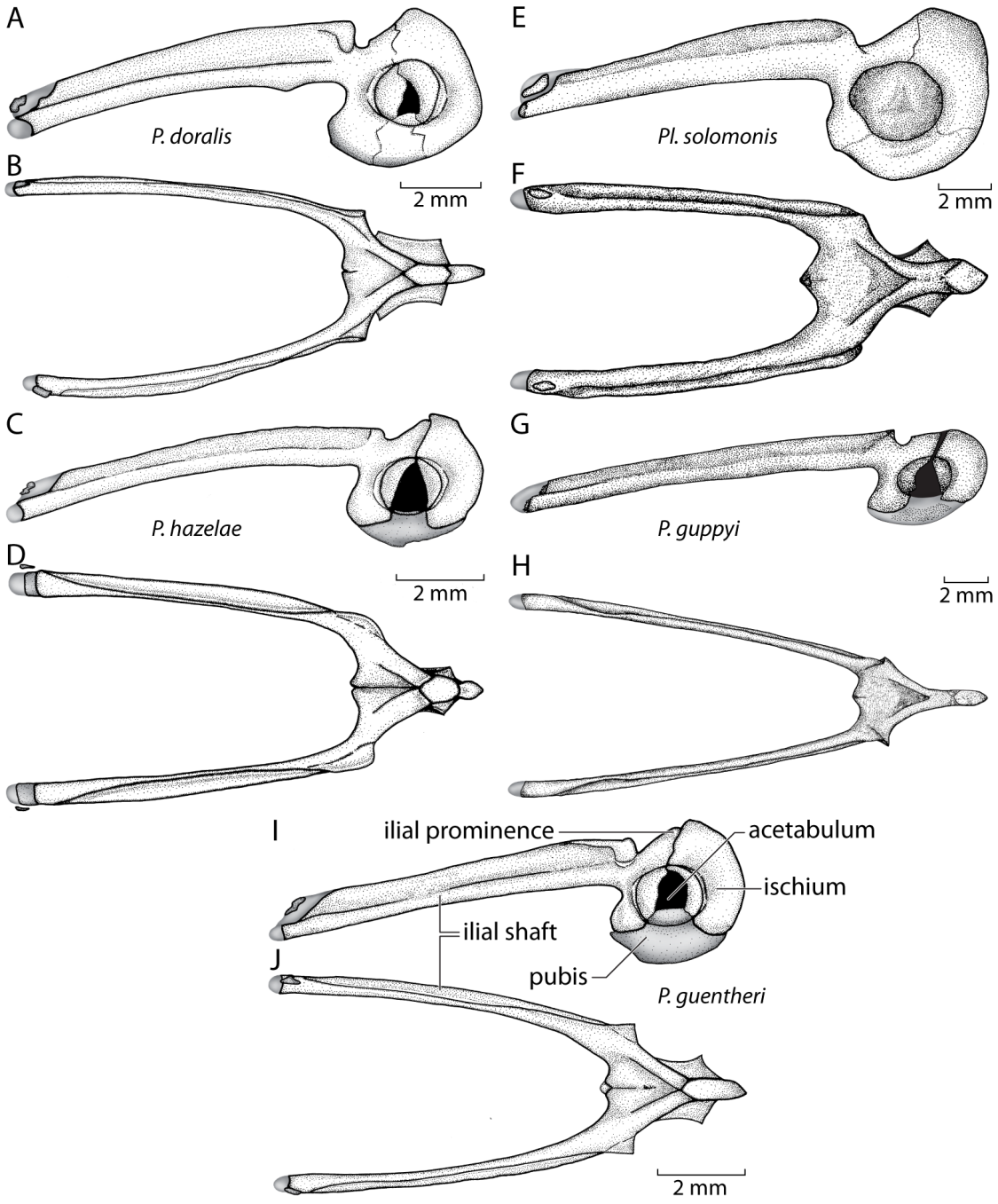

FIG. 19.—Pelvic girdles: *Platymantis dorsalis* (KU 313709) in lateral (A) and dorsal (B) aspects. *Platymantis hazelae* (KU 306739) in lateral (C) and dorsal (D) aspects. *Platymantis solomonis* (KU 307121) in lateral (E) and dorsal (F) aspects. *Platymantis guppyi* (KU 98161) in lateral (G) and dorsal (H) aspects. *Platymantis guentheri* (KU 319619) in lateral (I) and dorsal (J) aspects.

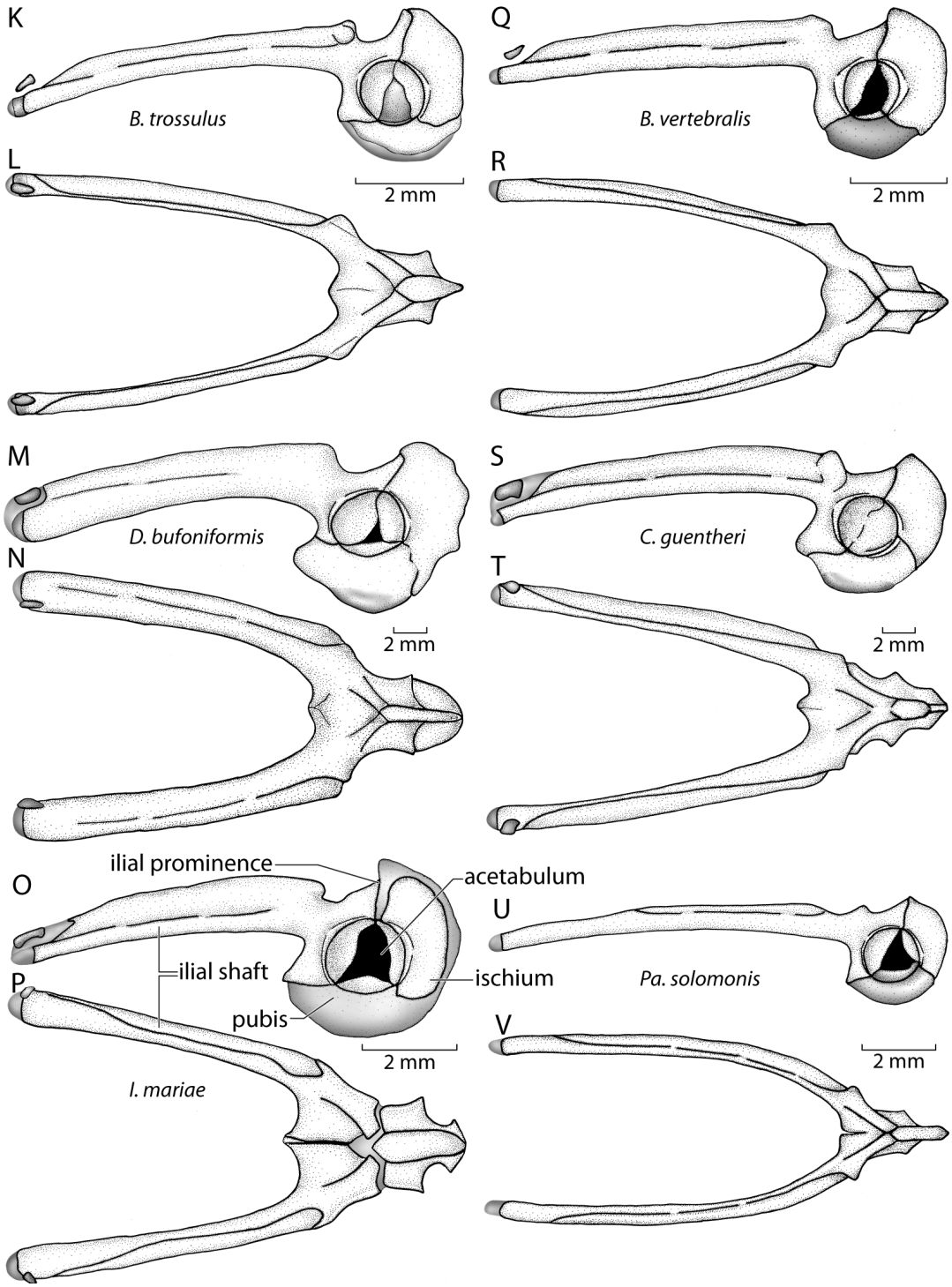

FIG. 20.—Pelvic girdles: *Batrachylodes trossulus* (KU 145134) in lateral (K) and dorsal (L) aspects. *Discodeles bufoniformis* (KU 307262) in lateral (M) and dorsal (N) aspects. *Ingerana mariae* (KU 309472) in lateral (O) and dorsal (P) aspects. *B. vertebralis* (KU 93735) in lateral (Q) and dorsal (R) aspects. *Ceratobatrachus guentheri* (KU 98467) in lateral (S) and dorsal (T) aspects. *Palmatorappia solomonis* (KU 93749) in lateral (U) and dorsal (V) aspects.

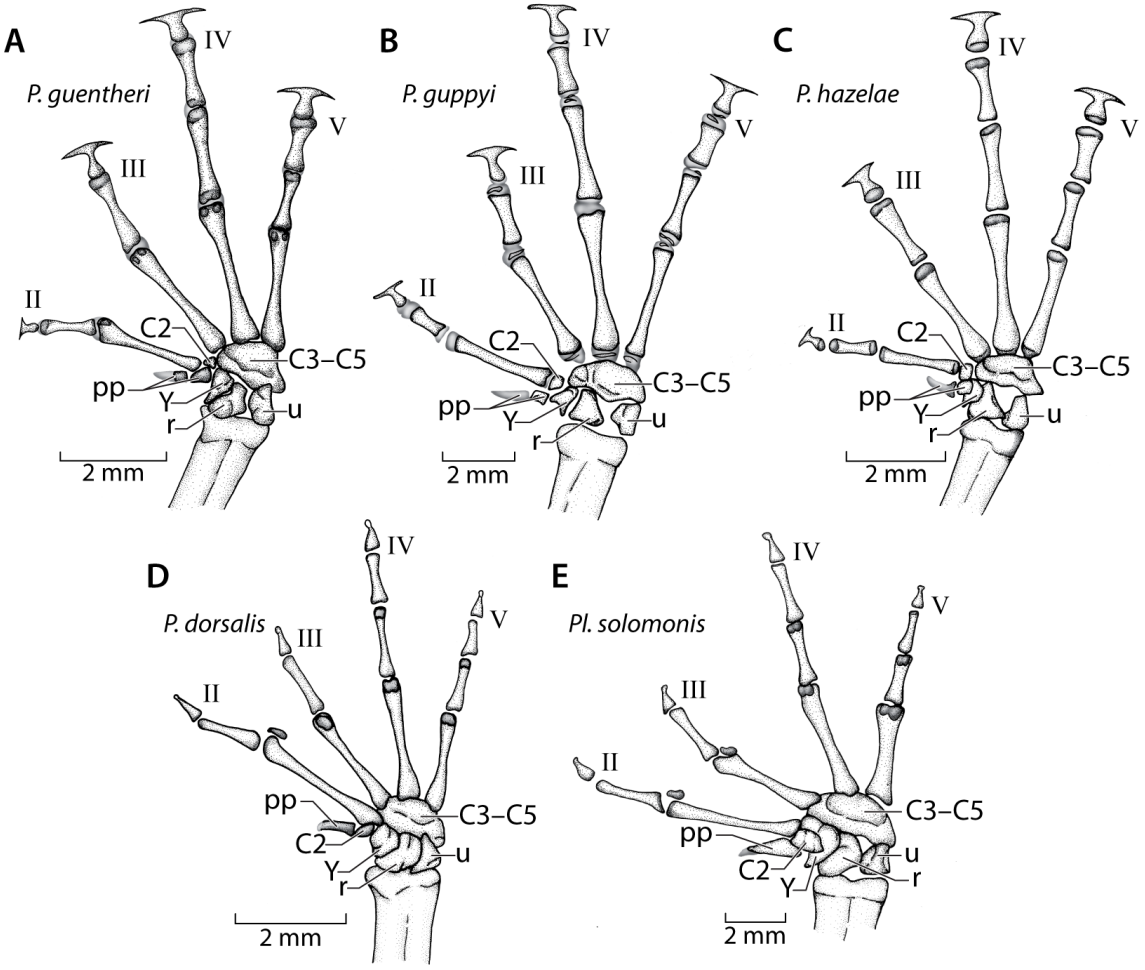

FIG. 21.—Ventral views of hands: A, *Platymantis guentheri* (KU 319619). B, *Platymantis guppyi* (KU 98161). C, *Platymantis hazelae* (KU 306739). D, *Platymantis dorsalis* (KU 313709). E, *Platymantis solomonis* (KU 307121). Black and white stipple represents bone, gray tone is cartilage, and stippling in gray represents mineralization of the cartilage. C1, Carpal 1; C2–4, Carpals 2–4; pp, prepollex; r, radiale; u, ulnare; Y, Element Y.

center of the acetabulum in *P. hazelae*, *P. dorsalis*, *P. guentheri*, *B. vertebralis*, *D. bufoniformis*, *Pa. solomonis*, and *I. mariae*. The acetabulum in *Platymantis guppyi* is not fused and has a triangular fenestra present in the center of the acetabulum. *Platymantis guppyi* has the least ossified acetabulum of all the taxa. *Discodeles bufoniformis* has an oval-shaped acetabulum whereas the other taxa have circular acetabulums.

Manus and pes (Figs. 22–27; Table 2).— The phalangeal formulae for the hands and feet

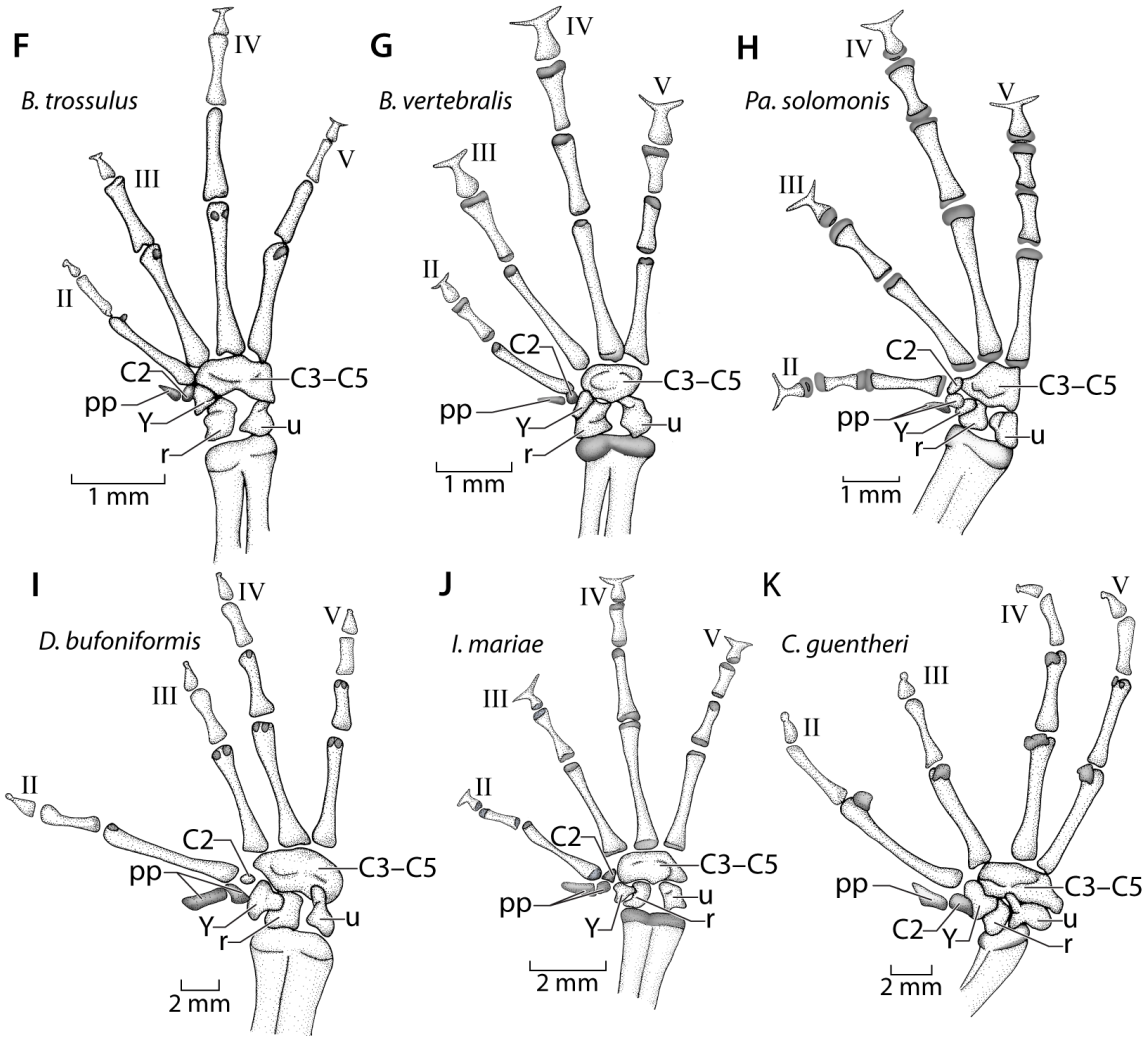

FIG. 22.—Ventral views of hands: F, *Batrachylodes trossulus* (KU 145134). G, *B. vertebralis* (KU 93735). H, *Palmatorappia solomonis* (KU 93749). I, *Discodeles bufoniformis* (KU 307262). J, *Ingerana mariae* (KU 309472). K, *Ceratobatrachus guentheri* (KU 98467). Black and white stipple represents bone, gray tone is cartilage, and stippling in gray represents mineralization of the cartilage. C1, Carpal 1; C2–4, Carpals 2–4; pp, prepollex; r, radiale; u, ulnare; Y, Element Y.

are standard—2-2-3-3 and 2-2-3-4-3, respectively, in all species. In increasing order of length, the order of the digits on the hand is: II-III-V-IV in *P. guppyi*, *P. hazelae, P. guentheri*, *B. trossulus*, *B. vertebralis*, *Pa. solomonis*, and *I. mariae*. In increasing order of length, the order of the digits on the hand is: III-V-II-IV for *Pl. solomonis*, *P. dorsalis*, *D. bufoniformis*, and *C. guentheri*. In increasing order of length, the order of the digits on the foot is: I-II-V-III-IV for all

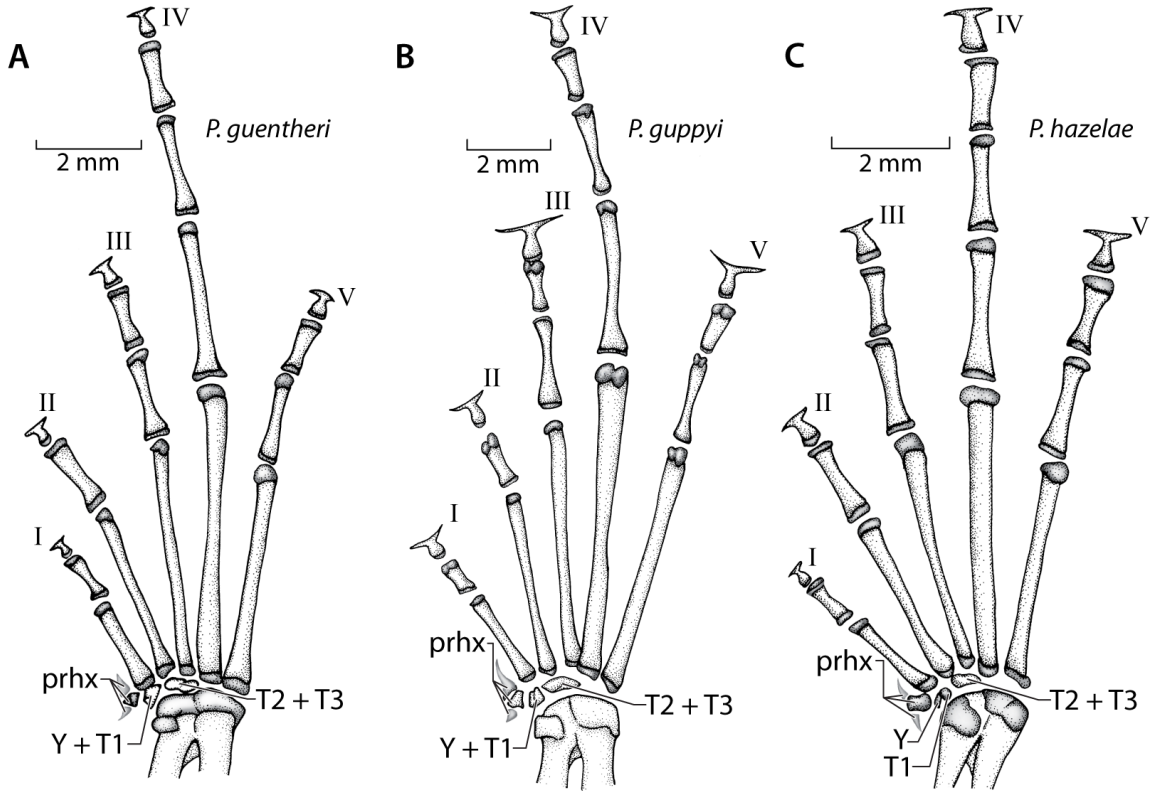

FIG. 23.—Ventral view of feet: A, *Platymantis guentheri* (KU 319619) left foot. B, *Platymantis guppyi* (KU 98161) left foot. C, *Platymantis hazelae* (KU 306739) right foot. Black and white stipple represents bone, gray tone is cartilage, and stippling in gray represents mineralization of the cartilage. T1, Tarsal 1; T2 + T3, Tarsals 2 and 3; Y, Element Y; Y + T1, Element Y and Tarsal 1.

taxa.

The carpus is composed of a radiale, ulnare, Element Y, Carpal 2, and a large postaxial element assumed to represent a fusion of Carpals 3–5 for all species. Element Y is moderately larger than Carpal 2 for all species.

The prepollex varies among these taxa. It is composed of two elements—one small proximal bone and an acuminate distal cartilage—in *P. guppyi*, *P. hazelae*, *P. guentheri*, *Pa. solomonis*, and *I. mariae*. The acuminate distal cartilage is mineralized at its base in *P. guentheri* and *P. hazelae*. The prepollex of *D. bufoniformis* is composed of two bones — one small

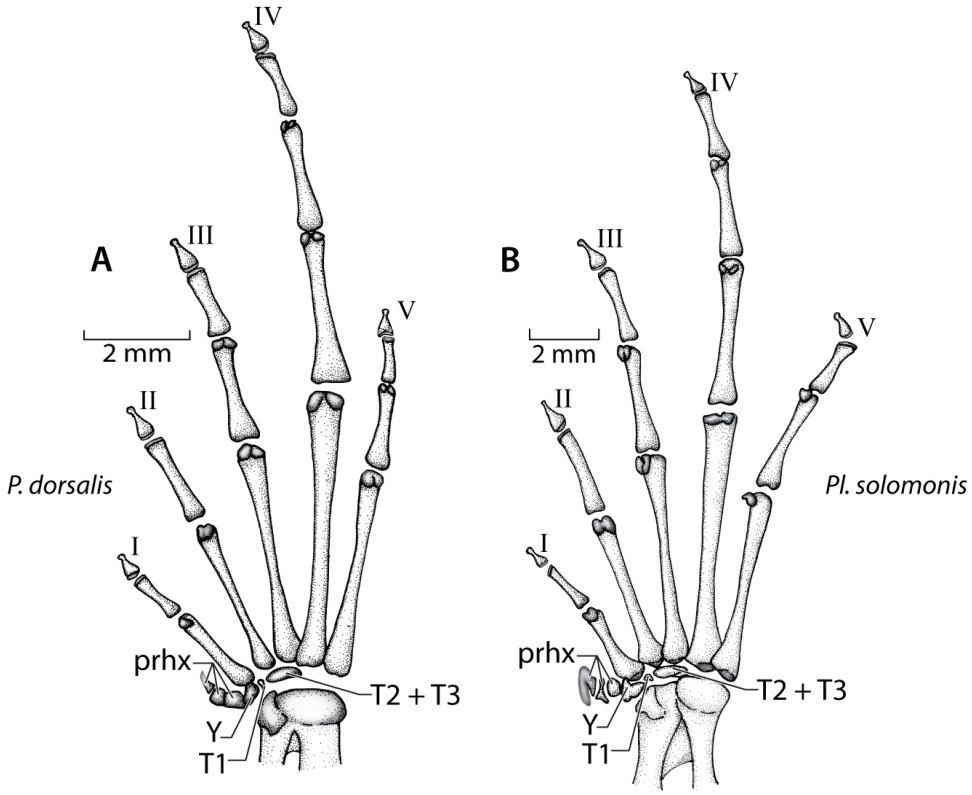

FIG. 24.—Ventral view of feet: A, *Platymantis dorsalis* (KU 313709) left foot. B, *Platymantis solomonis* (KU 307121) left foot. Black and white stipple represents bone, gray tone is cartilage, and stippling in gray represents mineralization of the cartilage. T1, Tarsal 1; T2 + T3, Tarsals 2 and 3; Y, Element Y; Y + T1, Element Y and Tarsal 1.

proximal bone and a larger, longer distal bone. The prepollex comprises one small proximal bone with acuminate distal cartilage in *B. trossulus* and *B. vertebralis*, In *P. dorsalis* and *Pl. solomonis,* the prepollex is composed of one long bone that is heavily mineralized with a small amount of acuminate distal cartilage; the prepollex of *C. guentheri* is similar but cartilage is absent distally.

The terminal phalanges are T-shaped in *P. guppyi*, *P. hazelae*, *P. guentheri*, *B. trossulus*, *B. vertebralis*, *Pa. solomonis*, and *I. mariae,* and have a small knob at the tips in *Pl. solomonis*, *P. dorsalis*, *C. guentheri*, and *D. bufoniformis*. Sesamoid bones are absent in the hands of *P. guppyi*, *P. hazelae*, *Pa. solomonis*, *B. vertebralis*, and *I. mariae,* but present at the metacarpal-

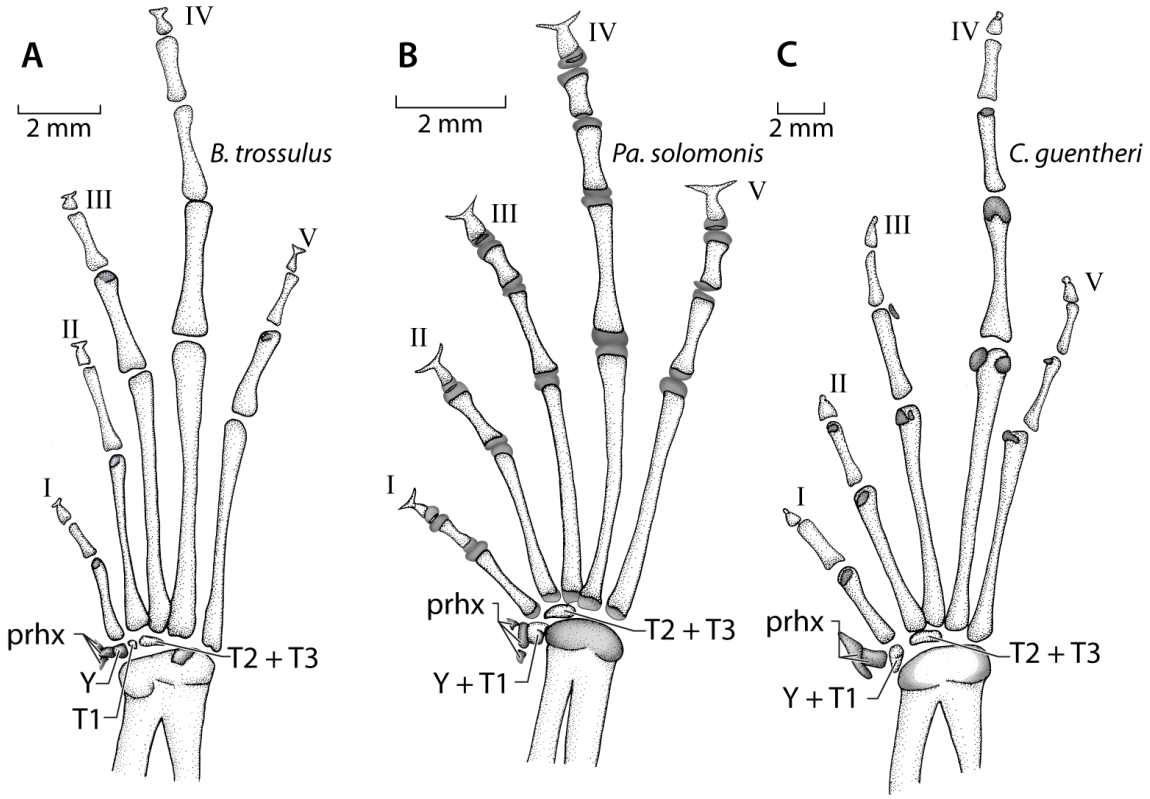

FIG. 25.—Ventral views of feet: A, *Batrachylodes trossulus* (KU 145134) mirror-reflection of right foot. B, *Palmatorappia solomonis* (KU 93749) mirror reflection of right foot. C, *Ceratobatrachus guentheri* (KU 98467) mirror reflection of right foot. Black and white stipple represents bone, gray tone is cartilage, and stippling in gray represents mineralization of the cartilage. T1, Tarsal 1; T2 + T3, Tarsals 2 and 3; Y, Element Y; Y + T1, Element Y and Tarsal 1.

phalangeal joint in Digits II–V in *P. dorsalis*, *Pl. solomonis*, *P. guentheri*, *C. guentheri*, *B. trossulus*, and *D. bufoniformis;* the sesamoids are larger in *P. dorsalis*, *Pl. solomonis*, and *C. guentheri* than *P. guentheri*, *D. bufoniformis*, and *B. trossulus*.

The tarsus is composed of two tarsal elements (Element Y + Tarsal 1 and Tarsal 2 + 3) in *P. guentheri*, *P. hazelae*, *P. guppyi*, *Pa. solomonis*, *C. guentheri*, and *I. mariae*, and three tarsal elements (Element Y, Tarsal 1 and Tarsal 2 + 3) in *Pl. solomonis*, *P. dorsalis*, *B. trossulus*, *B. vertebralis*, and *D. bufoniformis*. The prehallux is composed of a proximal bone and two distal cartilaginous elements in *P. guentheri*, *P. hazelae*, *P. guppyi*, *B. trossulus*, and *Pa. solomonis*, whereas there is one proximal mineralized element and one large cartilaginous distal element in

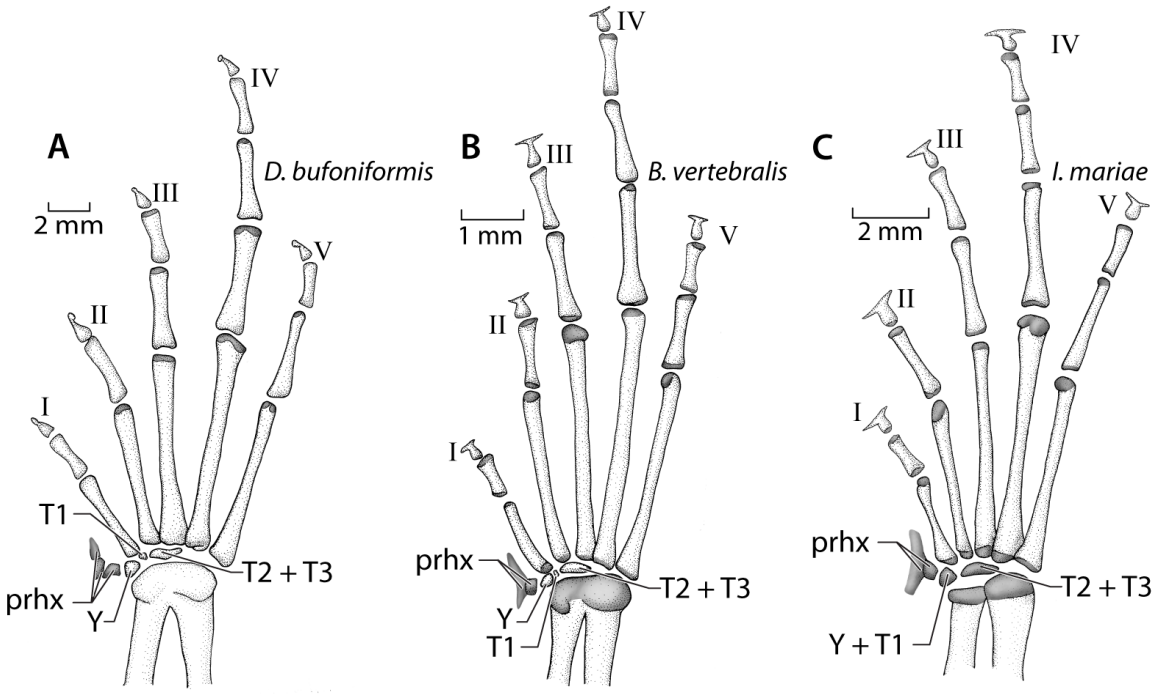

FIG. 26.—Ventral views of feet: A, *Discodeles bufoniformis* (KU 307262) left foot. B, *B. vertebralis* (KU 93735) left foot. C, *Ingerana mariae* (KU 309472) left foot. Black and white stipple represents bone, gray tone is cartilage, and stippling in gray represents mineralization of the cartilage. T1, Tarsal 1; T2 + T3, Tarsals 2 and 3; Y, Element Y; Y + T1, Element Y and Tarsal 1.

C. guentheri, *B. vertebralis*, and *I. mariae*. The prehallux comprises two heavily mineralized elements and one acuminate, distal cartilaginous element with some mineralization on its proximal edge in *P. dorsalis*, *Pl. solomonis*, and *D. bufoniformis*.

TABLE 2.—Summary of distribution of postcranial characters among Ceratobatrachine taxa (+ present, – absent). A, *Platymantis guentheri*; B, *Platymantis hazelae*; C, *Platymantis dorsalis*; D, *Platymantis solomonis*; E, *Platymantis guppyi*; F, *Batrachylodes vertebralis*; G, *Batrachylodes trossulus*; H, *Palmatorappia solomonis*; I, *Ceratobatrachus guentheri*; J, *Discodeles bufoniformis*; K, *Ingerana mariae*.

Character	Taxon										
	A	B	C	D	E	F	G	H	I	J	K
Vertebral Column											
Urostyle longer than presacral portion of vertebral column	–	–	–	–	+	–	–	–	–	–	–
Urostyle equal in length to presacral portion of vertebral column	–	–	–	–	–	+	–	+	–	–	–
Urostyle shorter than presacral portion of vertebral column	+	+	+	+	–	–	+	–	+	+	+
Dorsal crest bifurcated at anterior margin in dorsal view	–	+	–	–	–	–	–	–	–	–	–
Neural spines large & distinct	–	–	+	+	–	+	–	–	+	+	–
Sacrum narrower than all transverse processes	+	+	+	–	–	–	–	–	–	–	+
Sacrum equal in width to narrowest transverse processes	–	–	–	+	–	+	+	–	–	–	–
Neural spines present	+	+	+	+	+	+	+	–	+	+	+
Notch present on presacral II transverse process	–	–	–	+	+	–	–	–	+	+	–
Notch present on presacral III transverse process	–	–	–	+	–	–	–	–	–	–	–
Presacral II–IV transverse processes more robust	+	+	+	+	+	+	+	–	+	+	–
Irregular spurs present on transverse processes	–	–	+	+	–	–	–	–	–	+	–
Presacral III widest	+	+	+	+	+	+	+	+	+	+	+
Urostyle-sacrum bicondylar articulation	+	+	+	+	+	+	+	+	+	+	+
Pelvic Girdle											
Pubis completely ossified	–	–	+	+	–	–	–	–	+	+	–
Preacetabular angle less than 90°	–	+	–	+	–	+	–	–	+	+	–

Dorsolateral crests present	+	+	+	+	+	+	+	+	+	+	+
Ilial shafts long and slender (vs. more robust)	+	+	–	–	+	+	+	+	+	–	–
Fenestra absent in acetabulum	–	–	–	+	–	–	–	–	+	–	–
Pectoral Girdle											
Omosternum distal ramus longer than medial rami	–	–	+	+	+	+	+	–	+	+	+
Omosternum distal ramus same length as medial rami	+	+	–	–	–	–	–	+	–	–	–
Omosternum with fan-shaped cartilaginous plate	+	+	+	+	+	+	+	+	+	+	+
Omosternum bifurcated	+	+	+	+	+	+	+	+	+	+	+
Distal ramus of omosternum slightly expanded at anterior end	+	+	–	+	–	+	+	+	+	+	–
Pars acromialis same size as pars glenoidalis	+	+	–	–	–	–	–	–	+	+	–
Clavicle shafts straight & separated from base of omosternum	+	+	+	+	+	+	+	+	+	+	+
Clavicle oriented laterally (vs. posterolaterally)	+	–	+	+	+	+	+	–	+	+	+
Zonal medial length < girdle width between glenoid fossae	+	+	–	–	–	+	–	+	–	–	+
Coracoid midshaft width > 20% coracoid length	–	–	–	–	–	+	–	+	–	–	–
Coracoid midshaft width > 45% width of coracoid sternal end	–	–	–	–	–	+	–	+	–	–	–
Sternal fan-shaped cartilage plate present	+	+	+	+	+	+	+	+	+	+	+
Sternum distal ramus wider on anterior end	–	–	+	–	+	–	–	–	–	–	+
Pectoral fenestra more than twice as wide as high	–	–	–	–	–	+	–	+	–	+	+
Pectoral fenestra more than three times as wide as high	–	+	+	+	+	–	–	–	+	–	–
Pectoral fenestra more than four times as wide as high	+	–	–	–	–	–	+	–	–	–	–
Clavicle length greater than scapula length	–	–	–	–	+	+	+	–	–	–	–
Suprascapula highly ossified	–	–	+	–	+	–	–	–	–	+	–
Manus & Pes											

Phalangeal formula for hand 2-2-3-3	+	+	+	+	+	+	+	+	+	+	+
Phalangeal formula for hand 2-2-3-4-3	+	+	+	+	+	+	+	+	+	+	+
Increasing order of hand digit length, II-III-V-IV	+	+	–	–	+	+	+	+	–	–	+
Increasing order of foot digit length, I-II-V-III-IV	+	+	+	+	+	+	+	+	+	+	+
Carpals 3–5 fused	+	+	+	+	+	+	+	+	+	+	+
Prepollex composed of 2 elements	+	+	+	+	+	+	+	+	+	+	+
Element Y and Carpal 2 fused	–	–	+	+	–	+	+	–	+	–	–
Terminal phalanges T-shaped	+	+	–	–	+	+	+	+	–	–	+
Prehallux composed of 1 mineralized element	+	+	–	–	+	+	+	+	+	–	+
Sesamoid bones absent	–	+	–	–	+	+	–	+	–	–	+
Tarsus composed of two tarsal elements (vs. three)	+	+	–	–	+	–	–	+	+	–	+

Sexual Dimorphism

No sexual dimorphism in the skeletal structures was observed in those taxa for which there were both female and male specimens were available. Males of the genus *Batrachylodes* have been been reported to have a nasal plate that is absent in females (Norris, 2002). No nasal plates were observed in the specimens of *Batrachylodes* used for this study.

DISCUSSION

The skeletal diversity that is seen in these species of Ceratobatrachidae most likely resulted from a combination of both phylogenetic constraint and adaptation to different microhabitats. Further exploration of the phylogenetic constraint in Ceratobatrachidae would require placing this family and its osteology in a comparative phylogenetic context. Although recent molecular phylogenies agree upon which genera belong within Ceratobatrachidae, the position of the entire family within Raniodea is still unclear. Ceratobatrachidae has been shown to be sister to a variety of groups, including a clade containing Mantellidae, Rhacophoridae, Dicroglossidae, Ranidae, and Nyctibatrachidae, the family Ranixalidae, and the family Nyctibatrachidae (Bossuyt et al., 2006; Wiens et al., 2009; Pyron and Wiens, 2011). Until the sister family relationships are resolved, outgroup comparisons of Ceratobatrachidae with other anuran families and hypotheses of phylogenetic constraints cannot be properly addressed and character states cannot be properly polarized. Instead, osteological comparisons can be made between the arboreal, terrestrial, and semi-aquatic species, with the goal of identifying convergent characters that reflect adaptations to certain microhabitats.

The species of Ceratobatrachidae, like many different anuran groups, have successfully exploited a wide spectrum of ecological opportunities. Previous studies of anurans have shown clear form-function correlations between variation in morphology and locomotive, ecological,

reproductive, and feeding types (Zug, 1972; Emerson, 1978, 1979, 1982, 1983, 1984, 1985, 1991; Gray et al., 1997; Manzano, 2008; Gomes et al., 2009; Reilly and Jorgensen, 2011), therefore further explanation of what is known about the ecological types found within these frogs might help explain the patterns of osteological characters within the family. Additionally, the observation of apparent convergence in similar skeletal morphologies in species occupying similar microhabitats implies that some of these characters might be functionally relevant to the way in which a species exists in its microhabitat (Wainwright and Reilly, 1994).

The division of Philippine *Platymantis* into three well-defined species groups (Brown et al., 1997a,b, 1999; Alcala and Brown, 1999) represented the first attempt to partition ceratobatrachid diversity into a set of conveniently diagnosable morphological and ecological types (Brown, 2004). A preliminary analysis of morphological variation across the entire family suggested that it was possible to assign most species to a set of five ecomorph classes based on continuously varying morphometric traits and ecological characteristics, such as microhabitat and perch height (Brown, 2004). Results of the multivariate analyses of external morphology (plus consideration of microhabitat) led to definition of the five ecomorph types—two arboreal ecomorphs (large-bodied tree canopy species and small shrub frog species from cloud forests) and three terrestrial ecomorphs (common ground species, giants, and miniature species). Cloud forest shrub ecomorphs include many scansorial species that usually call from shrubs and understory vegetation (Brown et al., 1997a; Allison and Kraus, 2001; Brown, 2004). Large-bodied tree canopy specialist ecomorphs are also scansorial and have widely expanded terminal disks; these frogs call from high perches, the canopy strata, or aerial ferns. Terrestrial taxa usually call from the ground or in leaf litter (Brown, 2004). Semi-aquatic forms were previously thought to be limited to members of the genus of *Discodeles* and *Ingerana*, but additional semi-

aquatic members of *Platymantis* recently have been found in the Philippines, suggesting that a sixth ecomorph type might be identified in the future (Brown, *pers. comm.*) pending taxonomic work in progress.

Each ecomorph type defined above includes unrelated species from both the Philippine and the Papuan/Solomon-Bismarck radiations. Therefore, the evidence suggests that there have been multiple, independent evolutionary shifts among terrestrial, arboreal, and semi-aquatic ecomorph types in separate species radiations in Ceratobatrachidae (Brown, 2004; Menzies, 2006) (Fig. 28). The possible presence of adaptations in the anuran skeleton can be further investigated by comparing patterns of repeated osteological modifications in both radiations with the designated ecomorph type of the species (or, in other words, the microhabitat type of the species).

Although there is a large amount of variation in the crania, this variation appears uncorrelated with the microhabitat type. Sheil and Alamillo (2005) compared the skeleton of the terrestrial *Phyllomedusa atelopoides* with the arboreal *Phyllomedusa vaillanti* and found that the terrestrial species' cranium was slightly shorter than wide, the premaxillae were broad, the snout was flat and anterior, the frontoparietals articulated medially along entire length, appeared more ossified overall, and lacked a frontoparietal fenestra. The arboreal taxon's skull was wide as it was long, had a rounded snout formed by short, curved premaxillae, long slender frontoparietals that did not medially articulate and formed a frontoparietal fenestra (Sheil and Alamillo, 2005). Interestingly, I did not find similar character states in closely related arboreal-versus-terrestrial comparisons in ceratobatrachid species.

The morphological variation in the vertebral column, pelvic girdle, and pectoral girdle had weak or no apparent correspondence for the species' microhabitat. When dividing the eleven

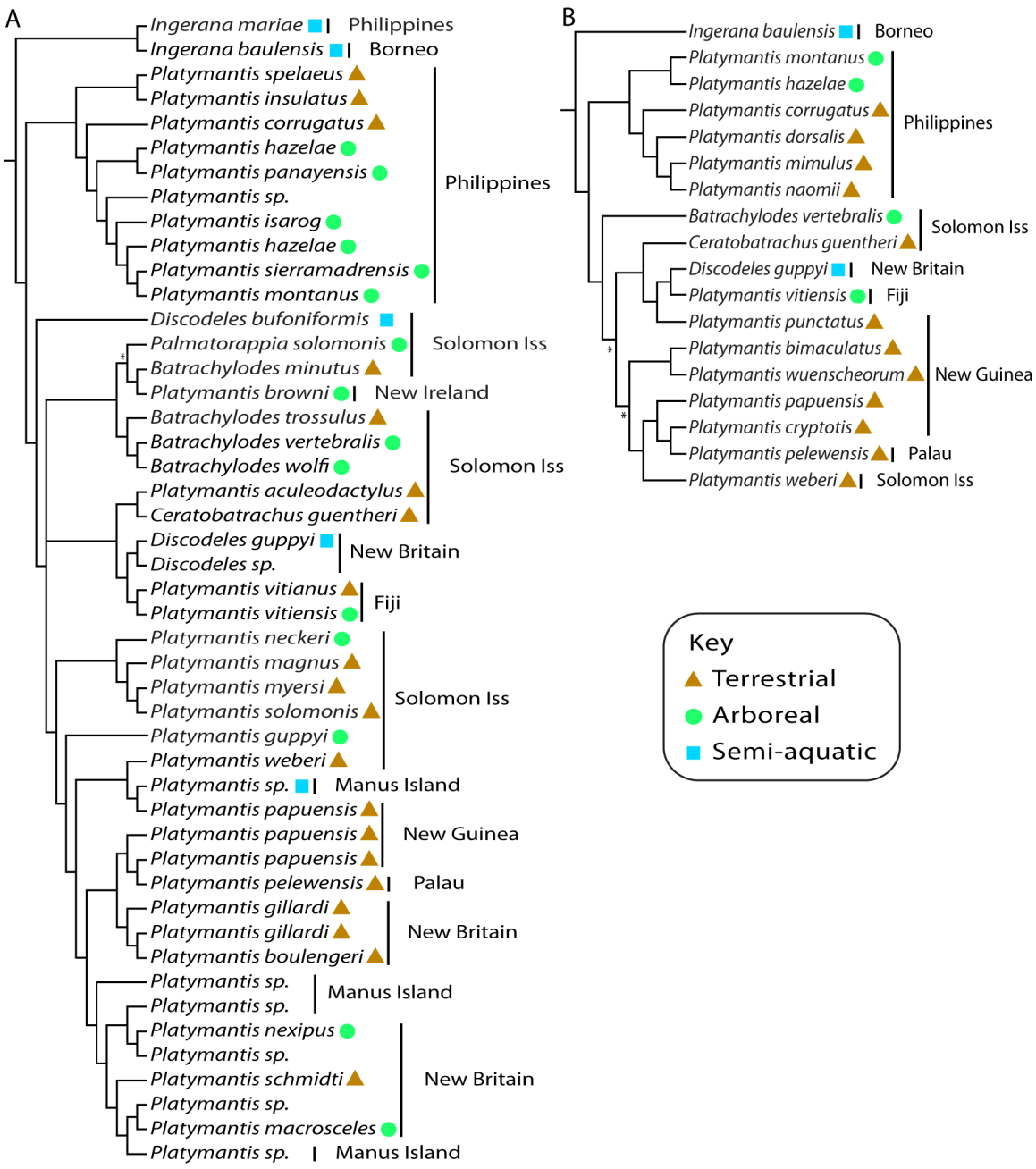

FIG. 27.—Cladograms depicting the phylogenetic relationships within Ceratobatrachidae redrawn from Brown (2004) (A) and Pyron and Wiens (2011) (B). Brown triangles indicate the species that are terrestrial ecomorphs, green circles indicate the species that are arboreal ecomorphs, and blue squares indicate species that are semi-aquatic or semi-semi-aquatic ecomorphs.

species into different groups based on their ecomorph type, there are no osteological characters that distinguish arboreal (*P. hazelae*, *Pa. solomonis*, *B. vertebtalis*, *P. guentheri* and *P. guppyi*), semi-aquatic (*D. bufoniformis* and *I. mariae*) and terrestrial species (*P. dorsalis*, *Pl. solomonis*, *B. trossulus*, and *C. guentheri*). If one excludes the two species of *Batrachylodes* (the smallest-bodied species examined) and *Ingerana mariae* (phylogenetically positioned outside of the clade contained the rest of Ceratbatrachidae) from consideration, some ecomorphological generalizations are possible. All three remaining terrestrial species have synostotically united exoccipitals. Neural spines are larger and more visible in the terrestrial and semi-aquatic species than in the arboreal species. The larger, more distinct neural spines found on the terrestrial and semi-aquatic species of Ceratobatrachidae also has an unknown functional consequence.
The pubis is completely ossified in terrestrial and semi-aquatic species, whereas those of the arboreal species are partially mineralized. With few exceptions, the terrestrial and semi-aquatic species had completely ossified pubes, while the pubes were not completely ossified in the arboreal species. The functional consequence of this amount of ossification is also unknown.

The elements of the hands and feet had the strongest correspondence to the microhabitat of the frog. The relative lengths of manus digits differ; in terrestrial and semi-aquatic species, the first digit is relatively longer than in arboreal species. The prepollex is composed of one element in the terrestrial species, but multiple elements in semi-aquatic and arboreal taxa. Cartilage is present in the distal element of the arboreal species, whereas the prepollex is entirely ossified in the semi-aquatic species. The terminal phalanges of the terrestrial and semi-aquatic species small knobs at the tips whereas arboreal species have T-shaped terminal phalanges. Kamermans and Vences (2007) surveyed 124 species of frogs across 64 genera to test the possible adaptive significance of osteological characters of the terminal phalanges and found a strong support for

the T-shaped terminal phalanges with climbing, arboreal, and rock-dwelling microhabitats. Earlier studies also hypothesized that the shape of the terminal phalanges correlated to the microhabitat of the frog (Drewes, 1984; Liem, 1970; Clarke, 1981; Emerson, 1991). The bifurcation of the terminal phalange evolved in arboreal and rock-dwelling frogs with enlarged disks. The bifurcation adds additional support to the enlarged disks and allows for additional muscle attachment for increase in disk mobility for improved climbing (Kamermans and Vences, 2009). The manus digit length order also sorted with microhabitat. No form-function or performance studies are published for frogs testing how digit lengths can affect the clinging or landing performance of anurans. It is possible that a longer Digit II is favorable for climbing or a shorter Digit II is favorable for non-scansorial movement on the ground.

In this study, it was found that the arboreal species possess a prepollex composed of two elements (one small proximal bone and an acuminate distal cartilage) while the terrestrial species have a prepollex composed of one element, and semi-aquatic species have a prepollex composed of two elements (one small proximal bone and a larger, longer distal bone). Some hylid treefrogs develop spines on the prepollex, rhacophorid treefrogs have enlarged prepollices and specialization of the prepollex is also known from nonarboreal frog species (Howes and Ridewood, 1888; Fabrezi, 2001; Lynch and Ruiz-Carranza, 1996; Lynch, 1993). The prepollex enlargement is possibly used in intrasexual aggression and has no known functional use linked to microhabitat (Kluge, 1981). The functional consequence to the variation in the number of elements in the prepollices in Ceratobatrachid frogs is unknown.

Sesamoid bones in the terrestrial species of Ceratobatrachidae were also commonly found. Sesamoid bones are skeletal elements that form within tendons or ligaments near bone joints or articulations. They can form in response to mechanical stress, but some can develop

without outside stress factors inducing their growth. The sesamoids of phalangeal joints aide in the gliding movement of surrounding tendons (Jerez et al., 2010; Ponssa et al., 2010). It is possible that the increase occurrence of sesamoid bones in the terrestrial species corresponds to an increase in stress or movement in the tendons of the hands when living on the ground.

If *Ceratobatrachus guentheri*—a highly modified leaf litter mimic species—also is removed from consideration, it is noted that irregular spurs occur only on the transverse processes of the two terrestrial species and the one semi-aquatic species. The functional consequence of the presence of spurs on the transverse process of the presacral vertebrae that were observed in the terrestrial species is unknown. The spurs possibly affect the epaxial musculature of the frog. Illial shafts are long and slender in the four arboreal species, whereas the semi-aquatic and terrestrial taxa have more robust illial shafts. The prehallux is composed of one mineralized element on the arboreal species, whereas it is composed of two heavily mineralized elements and one acuminate distal cartilaginous element with some mineralization on its proximal edge in the terrestrial and semi-aquatic species.

The lack of more morphological characters of the pelvic girdle, crania, pectoral girdle, and vertebral column corresponding to microhabitat could mean that the ecomorph categories, as they currently are defined, are too ambiguous to represent the locomotive modes of the species. For example, different functional skeletal morphologies can result in an arboreal frog being a strong jumper or a strong climber. In addition, it is conceivable that if cranial morphology is under selection by the surrounding environment, it may be exerted by predator and prey interactions, not by abiotic factors such as the microhabitat of the species. A previous anuran form-function study reported a correlation between jaw length and diet, and suggested that variation cranial morphology could be also correlated to feeding mode and possibly type of

biting defense (Emerson, 1985). In the pectoral girdle, the sternum is where the sternohyoideus muscle attaches; this muscle retracts the hyoid posteriorly (Emerson, 1977). The sternum also attaches to the sternoepicoracoideus muscle, which also attaches the style of the sternum to the epicoracoid plate of the pectoral girdle (Duellman and Trueb, 1994). This suggests that the variation in sternal and epicoracoid morphology could possibly correspond—like the cranial morphology—to feeding behavior rather than the microhabitat. Dietary information in Ceratobatrachidae is currently unknown and its possible correlation to cranial modifications warrant further investigation.

The type of iliosacral articulation (involving pelvic girdle lengths and presacral transverse processes) is correlated with different types of locomotor mode (Emerson, 1979; Emerson, 1982). The ridges of the pelvic elements allows for more muscle attachment, which contributes to saltatory locomotion in anurans (Emerson, 1978; Reilly and Jorgensen, 2011). Parts of the pectoral girdle morphology also affect movement of the frog. The omosternum serves as a part of the muscle attachment for the pars episternalis of the deltoideus muscle. The deltoideus muscle is active during both stance and swing phases of the forearms (Manzano et al., 2008). Generally, terrestrial frogs have shorter limbs and therefore tend to hop instead of jump. Arboreal species tend to be the best jumpers, and have relatively longer limbs (Emerson, 1978; Zug, 1972; Gomes et al., 2009). Some of the arboreal ceratobatrachids are known to be weak jumpers that move through their arboreal habitats often by crawling and grasping trunks, stems, and leaves of arboreal substrates (RMB, Pers. obs.).

Reilly and Jorgenson (2011) found that terrestrial jumpers tend to only have sagittal-hinge pelvic types, while arboreal jumpers appear to be more flexible in pelvic morphology. Arboreality has been accomplish four different ways in the pelvic bone of frogs (no change from

basal condition, addition of ridges on urostyle and ilia on the fore-aft slider or lateral-bender pelvic, cartilangeous flat-sided sacra, or retention of the sagittal-hinge pelvic), suggesting that toepads, relative limb length or another morphological trait might be more important in adapting to an arboreal habitat than their pelvic type. All Ceratobatrachid species have retained sagittal-hinge pelvic type with rod-like diapophyses and ridges on ilia and urostyles, which is known to occur both in arboreal and terrestrial jumpers.

More data regarding the amount of climbing, jumping, hopping, crawling, and swimming, and feeding should be collected in order to further explore the correlation between osteology and ecology of a frog species.

CONCLUSION

Ceratobatrachidae is an osteologically diverse family of Melanasian forest frogs. These direct developers have successful radiated in both the Philippines and the Papuan/Solomon-Bismarck islands, into arboreal, terrestrial, and semi-aquatic microhabitats. When investigating the possible ties between morphology and ecology, definition of frogs as simply "arboreal" or "terrestrial" can be ambiguous. Nevertheless, for Ceratobatrachidae, the obligatory morphological changes for switching between arboreal and terrestrial lifestyles clearly involve specializations of the hands and feet. However, repeated changes in the pectoral and pelvic girdles and the vertebral column may be more relevant to the transition between locomotive modes that do not correlate to the current microhabitat categories. The variation in the cranium and the sternum could potentially be correlated to shifts in diets that also do not correlate to these microhabitat categories. Further research in the osteological adaptations requires more ecological data, such as locomotive mode and diet behavior, to obtain a more complete picture of the interaction between the ecology and morphology of these frogs. Future research on

Ceratobatrachidae should try to finish resolving the phylogenetic relationships so that the dynamic between phylogenetic constraints and adaptation can also be explored.

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APPENDICES

APPENDIX 1.—List of currently described species of Ceratobatrachidae and their known distributions.

Species	Distribution
Batrachylodes elegans Brown and Parker, 1970	Solomon Islands
Batrachylodes gigas Brown and Parker, 1970	Solomon Islands
Batrachylodes mediodiscus Brown and Parker, 1970	Solomon Islands
Batrachylodes minutus Brown and Parker, 1970	Solomon Islands
Batrachylodes montanus Brown and Parker, 1970	Solomon Islands
Batrachylodes trossulus Brown and Myers, 1949	Solomon Islands
Batrachylodes vertebralis Boulenger, 1887	Solomon Islands
Batrachylodes wolfi (Sternfeld, 1920)	Solomon Islands
Ceratobatrachus guentheri Boulenger, 1884	Solomon Islands
Discodeles bufoniformis (Boulenger, 1884)	Solomon Islands
Discodeles guppyi (Boulenger, 1884)	Solomon Islands; Bismarck Archipelago
Discodeles malukuna Brown and Webster, 1969	Solomon Islands
Discodeles opisthodon (Boulenger, 1884)	Solomon Islands
Discodeles vogti (Hediger, 1934)	Bismarck Archipelago
Ingerana baluensis (Boulenger, 1896)	Borneo
Ingerana mariae (Inger, 1954)	Philippines
Palmatorappia solomonis (Sternfeld, 1920)	Solomon Islands
Platymantis acrochordus (Brown, 1965)	Solomon Islands
Platymantis aculeodactylus Brown, 1952	Solomon Islands
Platymantis adiastolus Brown, Richards, Sukumaran, and Foufopoulos, 2006	Bismarck Archipelago
Platymantis admiraltiensis Richards, Mack, and Austin, 2007	Bismarck Archipelago
Platymantis akarithymus Brown and Tyler, 1968	Bismarck Archipelago
Platymantis banahao Brown, Alcala, Diesmos, and Alcala, 1997	Philippines
Platymantis batantae Zweifel, 1969	New Guinea
Platymantis bayani Siler, Alcala, Diesmos, and Brown, 2009	Philippines
Platymantis biak Siler, Diesmos, Linkem, Diesmos, and Brown, 2010	Philippines
Platymantis bimaculatus Günther, 1999	New Guinea
Platymantis boulengeri (Boettger, 1892)	Bismarck Archipelago
Platymantis browni Allison and Kraus, 2001	Bismarck Archipelago
Platymantis bufonulus Kraus and Allison, 2007	Bismarck Archipelago
Platymantis caesiops Kraus and Allison, 2009	New Guinea
Platymantis cagayanensis Brown, Alcala, and Diesmos, 1999	Philippines
Platymantis cheesmanae Parker, 1940	New Guinea
Platymantis cornutus (Taylor, 1922)	Philippines
Platymantis corrugatus (Duméril, 1853)	Philippines
Platymantis cryptotis Günther, 1999	New Guinea
Platymantis desticans Brown and Richards, 2008	Solomon Islands
Platymantis diesmosi Brown and Gonzalez, 2007	Philippines
Platymantis dorsalis (Duméril, 1853)	Philippines
Platymantis gilliardi Zweifel, 1960	Bismarck Archipelago
Platymantis guentheri (Boulenger, 1882)	Philippines

Platymantis guppyi (Boulenger, 1884)	Solomon Islands
Platymantis hazelae (Taylor, 1920)	Philippines
Platymantis indeprensus Brown, Alcala, and Diesmos, 1999	Philippines
Platymantis insulatus Brown and Alcala, 1970	Philippines
Platymantis isarog Brown, Brown, Alcala, and Frost, 1997	Philippines
Platymantis latro Richards, Mack, and Austin, 2007	Bismarck Archipelago
Platymantis lawtoni Brown and Alcala, 1974	Philippines
Platymantis levigatus Brown and Alcala, 1974	Philippines
Platymantis luzonensis Brown, Alcala, Diesmos, and Alcala, 1997	Philippines
Platymantis macrops (Brown, 1965)	Solomon Islands
Platymantis macrosceles Zweifel, 1975	Bismarck Archipelago
Platymantis magnus Brown and Menzies, 1979	Bismarck Archipelago
Platymantis mamusiorum Foufopoulos and Brown, 2004	Bismarck Archipelago
Platymantis manus Kraus and Allison, 2009	Bismarck Archipelago
Platymantis megabotoniviti† Worthy, 2001	Fiji
Platymantis mimicus Brown and Tyler, 1968	Bismarck Archipelago
Platymantis mimulus Brown, Alcala, and Diesmos, 1997	Philippines
Platymantis montanus (Taylor, 1922)	Philippines
Platymantis myersi Brown, 1949	Solomon Islands
Platymantis nakanaiorum Brown, Foufopoulos, and Richards, 2006	Bismarck Archipelago
Platymantis naomii Alcala, Brown, and Diesmos, 1998	Philippines
Platymantis neckeri (Brown and Myers, 1949)	Solomon Islands
Platymantis negrosensis Brown, Alcala, Diesmos, and Alcala, 1997	Philippines
Platymantis nexipus Zweifel, 1975	Bismarck Archipelago
Platymantis paengi Siler, Linkem, Diesmos, and Alcala, 2007	Philippines
Platymantis panayensis Brown, Brown, and Alcala, 1997	Philippines
Platymantis papuensis Meyer, 1875	New Guinea; Bismarck Archipelago
Platymantis parilis Brown and Richards, 2008	Solomon Islands
Platymantis parkeri (Brown, 1965)	Solomon Islands
Platymantis pelewensis Peters, 1867	Palau
Platymantis polillensis (Taylor, 1922)	Philippines
Platymantis pseudodorsalis Brown, Alcala, and Diesmos, 1999	Philippines
Platymantis punctatus Peters and Doria, 1878	New Guinea
Platymantis pygmaeus Alcala, Brown, and Diesmos, 1998	Philippines
Platymantis rabori Brown, Alcala, Diesmos, and Alcala, 1997	Philippines
Platymantis schmidti Brown and Tyler, 1968	Bismarck Archipelago
Platymantis sierramadrensis Brown, Alcala, Ong, and Diesmos, 1999	Philippines
Platymantis solomonis (Boulenger, 1884)	Solomon Islands; Bismarck Archipelago
Platymantis spelaeus Brown and Alcala, 1982	Philippines
Platymantis subterrestris (Taylor, 1922)	Philippines
Platymantis sulcatus Kraus and Allison, 2007	Bismarck Archipelago
Platymantis taylori Brown, Alcala, and Diesmos, 1999	Philippines
Platymantis vitianus (Duméril, 1853)	Fiji
Platymantis vitiensis (Girard, 1853)	Fiji
Platymantis weberi Schmidt, 1932	Solomon Islands
Platymantis wuenscheorum Günther, 2006	New Guinea

APPENDIX 2. —Specimens Examined.

Platymantis guentheri.— PHILIPPINES: AGUSAN DEL SUR PROVINCE: *Municipality of San Francisco*: Barangay Bagusan II, Mt. Magdiwata: KU 319619 ♂ and KU 319614 ♀. *Platymantis hazelae*.— PHILIPPINES: NEGROS ORIENTAL PROVINCE: *Municipality of Valencia*: Barangay Lunga, Mt. Talinus: KU 306743 ♂ and KU 306739 ♀. *Platymantis dorsalis*.— PHILIPPINES: CAMARINES NORTE PROVINCE: *Municipality of Labo*: Barangay Tulay Na Lupa, Mt. Labo camp 1: KU 313709 ♂ and KU 313717 ♀. *Platymantis solomonis*.— SOLOMON ISLANDS: LOLA ISLAND: *Western Province*: Lola Island, Zipolo Habu Resort: KU 307121 ♂ and KU 307118 ♀. *Platymantis guppyi*.— PAPUA NEW GUINEA: BOUGAINVILLE: *Kunua*: KU 98161 ♂ and KU 98165 ♀. *Ingerana mariae*.— PHILIPPINES: PALAWAN PROVINCE: *Municipality of Brooke's Point*: Barangay Samarinana Mt. Montalingahan Range, Area "Pitang": KU 309472 ♂. *Palmatorappia solomonis*.— PAPUA NEW GUINEA: BOUGAINVILLE: Kunua: KU 93749 ♀. *Batrachylodes trossulus*.— PAPUA NEW GUINEA: BOUGAINVILLE: *Mutahi*: KU 145134 ♀. *Batrachylodes vertebralis*.— PAPUA NEW GUINEA: BOUGAINVILLE: *Kunua*: KU 93735 ♂. *Discodeles bufoniformis*.— SOLOMON ISLANDS: RANONGGA ISLAND: *Ranongga Island, Village of Poroi*: KU 307262 ♂. *Ceratobatrachus guentheri*.— PAPUA NEW GUINEA: BOUGAINVILLE: Kunua: KU 93735 ♂.